

BEHAVIOR OF THE HAWAIIAN SPINNER DOLPHIN, *STENELLA LONGIROSTRIS*

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ABSTRACT

The Hawaiian spinner dolphin, *Stenella longirostris*, was recorded from Kure Atoll to the island of Hawaii. It enters atoll lagoons or specific coves or swims over shallow sandy areas, usually near deep water, to rest. Access to nighttime feeding grounds may regulate the location of these rest areas. Rest areas are generally 50 meters or less in depth.

Natural scars and marks allowed study of movements and school structure. Schools are fluid assemblages of variable size and composition. Only small subgroups within schools may have long-term integrity.

Spinner dolphins exhibit several aerial patterns including spinning which is mostly associated with sound production upon reentry, and each is typical of a specific school activity level. Sounds may serve as omnidirectional sound sources maintaining school cohesion beyond the limits of vision.

The daily cycle of spinner dolphins consists of nighttime feeding, morning approach to shore, morning-midday rest, and travel to feeding grounds near dusk. Feeding is upon scattering layer fishes, squid, and shrimp.

Dolphins very commonly show scars from large sharks and from the small squaloid shark, *Isistius brasiliensis*, which scoops disc-shaped pieces of blubber from them. These wounds heal to form dollar-shaped scars.

Most that is known in any depth about the behavior of dolphins has come from observations of captive animals. Yet the environment of captivity, which is at best a pool a few dozen meters in longest dimension and 5 or 10 m deep, can allow only certain aspects of normal behavior to occur. Intragroup relationships may persist, but are usually distorted because relationships seldom remain intact. At best only hints of normal movement and activity patterns can persist where feeding schedules are determined by the workdays of trainers. In nature spinner dolphins, at least, travel constantly, even during rest. Dolphins of many species dive and feed in very deep water.

Thus, however difficult it might be, the naturalist who would study dolphin behavior feels the need to study them in nature. It is usually no simple task. They are wary and travel many kilometers in a day. The presence of the observer almost inevitably causes bias. Dolphins hear exceedingly well, and dolphin schools may be aware of an approaching ship a kilometer or more away.

Our first 2-yr effort (1968-69), with a spotted, or "kiko," dolphin, *Stenella attenuata*, school which we knew to frequent the area within a few

kilometers of Kaena Point, Oahu, Hawaii, was abandoned for the reasons mentioned above. It simply proved too expensive in time, money, and effort to work with the animals. Our work was never free from observer bias. Reports of a school of the spinner dolphin, *Stenella longirostris*, (Schlegel 1841), living permanently in Kealakekua Bay, on the Kona or lee coast of the island of Hawaii, caused us to visit the area to see if work was feasible. We found an unusual situation in which several vexing observational problems were ameliorated.

Spinner dolphins do occur in Kealakekua Bay frequently (our figures indicate occupancy about 74% of the time). The bay itself is remarkably good for observation. The Kona coast is normally quite calm, especially in morning hours. Lateral visibility is usually 20 m or more. The local people seldom disturb the dolphins. Only cruise boats, which seek out the schools and run through them, are a predictable disturbance. An abrupt 150 m lava cliff backs the bay. Schools sometimes came close to the cliff base at places where our visibility was blocked and could not be seen from the clifftop. But, most of the time we could watch wholly undisturbed schools at reasonably close range, although the distance proved too long for individual identification, and the lack of contrast between animal

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and background defeated good photography. Finally, the bay is relatively small, 3.2 km across its mouth and indented about 2.5 km deep. Its entire area was visible from the cliff top, and usually visibility was good enough that one could see schools well beyond its confines (Figure 1).

These unusual circumstances allowed us to gather new information about spinner dolphin behavior, especially about the diurnal cycle and patterns of movement, though some difficult observational problems remain.

Spinner dolphins proved exceptionally interesting, observational subjects. Not only do they "spin" or leap from the water and revolve rapidly around their longitudinal axis, but they also perform other aerial behavior that can be observed from a considerable distance. These bits of aerial behavior and the sequence in which they occurred proved to be a key to what one might call the emotional or activity level of the school. This level in turn is closely correlated with a number of features of dolphin life, especially the regular sequence of activities during a daily cycle. Aerial

behavior, once understood, becomes a predictor of daily activity patterns.

This work, performed in 1970-73, represents a beginning analysis of natural spinner dolphin behavior, a field still in its infancy. Previous reports of the behavior of wild dolphin schools have been mostly single or very fragmentary observations (see Norris and Dohl in press for a review). A few detailed studies exist and allow comparison with this work, such as the work performed by Saayman and Tayler (1971); Saayman, Bower, and Tayler (1972); Tayler and Saayman (1972); and Saayman, Tayler, and Bower (1973), and more recently by Würsig and Würsig (1977); Shane (1977); Würsig (1978); Wells et al. (in press). Saayman and Tayler have analyzed the daily movements of the bottlenose dolphin, *Tursiops aduncus*, and the Indopacific humpback dolphin, *Sousa teuszii*, and their feeding formations and strategies for fish crowding and capture. Würsig's studies concentrated on Argentinian populations of *Lagenorhynchus obscurus* and *T. truncatus*, while Wells et al. work dealt with *T. truncatus* in Florida.

There are parallels in these works with the behavior patterns described here. The recent work by the Würsigs on the group size, composition, and stability of bottlenose dolphin schools bears similarity. Like ours, much of this work was performed from cliff top observation posts using natural scars and marks to identify individuals. Shane's study, also on bottlenose dolphins, utilized natural scars and marks. Wells et al. carried out extensive tagging studies on Florida bottlenose dolphins. All of these studies and that reported here show remarkable fluidity in school composition and size over short periods of time. The dolphin populations that have been studied, it seems, are not composed of discrete schools of modest size but instead of highly fluid groups that may range considerable distances and may be found associated in very variable combinations of individual animals.

Morphology

Hawaiian spinner dolphins are moderate-sized, slim-bodied, and long-beaked odontocete cetaceans. Adults reach at least 2 m TL (total length), and about 55-62 kg (Perrin 1975). They are handsomely marked animals with a dark gray cape over the dorsal surface, a light gray lateral field (using the terminology of Perrin 1972) sharply demarcated from the cape above, and the white

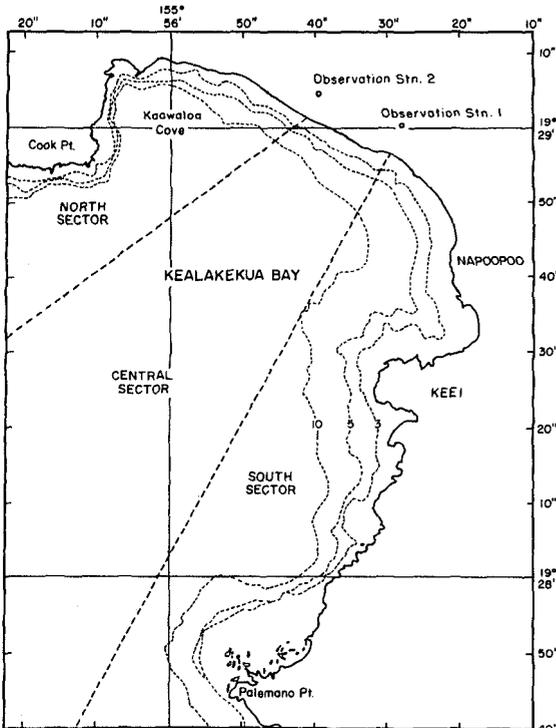


FIGURE 1.—Kealakekua Bay, Hawaii. Shown are observation posts on cliff that backs the bay, shallow-water areas (in meters), and approximate areas frequented by resting schools of spinner dolphins. Also indicated are arbitrary bay sectors used in analysis of arrival and departure directions.

belly below. The white of the belly extends up the flanks to about the level of the eye. The beak, or rostrum, is dark gray, tipped prominently with black; the lip margins are dark; and the ventral surface of the beak is white. The pectoral fins are dark gray, and a dark flipper band connects its anterior insertion to the eye, which is surrounded by a black eyepatch. Flukes and dorsal fin are dark gray. These color pattern components have been described in more detail by Perrin (1972), and they have been compared with the patterns of geographical forms of spinner dolphins living in the eastern tropical Pacific. In nature, against the blue or turquoise backdrop of tropical water, the dark pattern components of spinner dolphins appear in shades of brown, but the effect is usually lost when the animals are removed from the water. The white and other pattern marks are often suffused with pink, from superficial blood flow in the blubber, which may also contribute to the overall brownish cast of pattern components in living spinners.

Systematics

In recent years a worldwide picture of the distribution and systematics of tropical odontocetes has begun to emerge. Well-documented collections, often with measurements and photographs, have been made from all oceans, especially where dolphins are involved in fishery operations (Kasuya et al. 1974; Perrin 1975). A special beneficiary of this work has been the once chaotic genus *Stenella*. It now seems reasonably clear that the genus is composed largely of three major species or species complexes: the spinner dolphins, allied to *S. longirostris* of the Hawaiian Islands; the striped dolphin, *S. coeruleoalba*; and the spotted dolphins, allied to *S. attenuata* of the Hawaiian Islands. All are tropical or subtropical. All are often found far offshore or near islands.

In the eastern and central Pacific, Perrin (1975) discerned four geographical forms of spinner dolphins: 1) a Costa Rican long-snouted form occurring close to the Central American coast, 2) an eastern form occupying the open sea from the American coast out to long. 115° W, 3) a whitebelly form occupying the open ocean both south and west of the eastern form (and overlapping with it to some extent) to about long. 145° W and nearly to lat. 5° S, and 4) an Hawaiian form localized around the Hawaiian island chain. Perrin (1975) stated that Hawaiian spinner dolphins are most

closely related to the adjacent whitebelly form, differing from them by being somewhat more robust, by having a larger area of white belly coloration, and by lacking the speckled margins of the white belly field. He places the complex tentatively in the species *S. longirostris*.

Most of the races of spinner dolphins from around the world are quite similar to the Hawaiian form. Only the Costa Rican and eastern forms are strikingly different, being nearly uniform gray, with faint hints of pattern components found in other races. These aberrant forms also show remarkable sexual dimorphism, which is otherwise rather subtle throughout the species. Fully adult males of these two races often possess a dorsal fin that is canted sharply forward, "like it was stuck on backward," and a very heavy post-anal protuberance. The fin of Hawaiian spinner dolphins is either triangular or very slightly falcate, and only a subtle postanal protuberance can be noted in adult males.

METHODS

A camp was established on the Greenwell Ranch at the edge of the cliff overlooking Kealakekua Bay (Figure 1). Two observation sites were used for recording and observation by telescopic means. Observer teams kept regular watches during daylight hours.

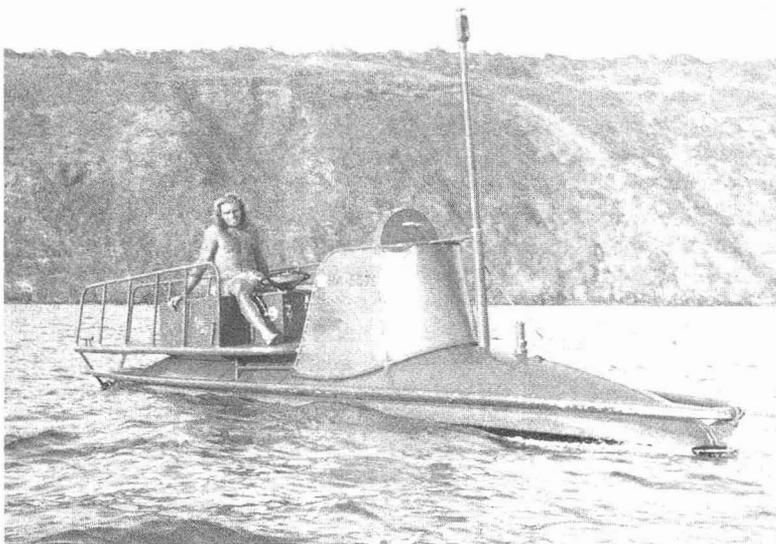
Several vessels were used for observations at sea, or to provide an anchored platform in the bay, including the brigantine *Westward* and the motor sailers RV *Hikino* and the RV *Imua*. A trip through the northwest Hawaiian chain was made on the U.S. Coast Guard buoy tender *Buttonwood*.

Fourteen spotting flights were made throughout the main Hawaiian chain, mostly from small fixed wing aircraft.

Underwater observations were made in a specially built underwater observation vehicle or mobile observation chamber (MOC) 6 m long, which looked like a small submarine (Figure 2) but did not submerge. It consisted of a float made from an auxiliary aircraft gasoline tank and a central observation chamber. The viewer in this chamber below water obtained ventilation from a squirrel cage blower and was surrounded by a band of Plexiglas² windows at eye height. Controls for turning or tilting the craft were at hand, and a

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

FIGURE 2.—Mobile observation chamber (MOC) at Kealakekua Bay. The hatch is open to a cylindrical observation chamber that projects 1.5 m below the hull. The observer views through a 360° band of Plexiglas windows. The operator steers and operates the engine.



tape recorder was connected to a hydrophone³ mounted amidships and oriented forward.

The craft was run by an outboard engine set in a well aft. Stability was maintained by 900 kg of lead blocks in a compartment below the observers feet.

Other underwater observations were made with scuba, or by putting an observer with snorkle or scuba below the bow of a slowly moving skiff, holding onto a bow painter. In this way the observers could sometimes be towed among the animals and even be jostled by them. A field station was established at the village of Napoopoo on Kealakekua Bay.

Feeding was observed from skiffs and larger vessels. Dip net samples were taken in the region of feeding, and stomach analysis of such specimens as became available to us were collected. The squid and crustaceans in stomach samples were identified by Richard Young of the Department of Oceanography, University of Hawaii. Fish otolith collections were lost through improper preservation.

Recordings were made with a hydrophone deployed from a stationary skiff located near a school of animals or from the MOC. Monitoring was by use of headphones. During our studies we were fortunate to have William Schevill and William Watkins of the Woods Hole Oceanographic In-

stitution establish a four-hydrophone array deep in Kealakekua Bay. With this apparatus, three-dimensional tracks of passing dolphins were obtained that were of greater range and fidelity than allowed by our simple gear. The experimental arrangement of this array and recording characteristics are described in Watkins and Schevill (1974).

Dolphin radiotracking used dolphin dorsal fin radios (see Evans 1974) and a hand-held direction finder. Dolphins were captured by a standard head net.

Throughout this paper we use the term "school" to indicate all animals in a discrete area that move together. Such schools are often composed of recognizable, discrete "groups" of animals clustered together and moving and diving more or less in unison. For instance, while the direction of movement of larger schools may be the same for all its parts, diving synchrony for all animals may be quite extended and ragged, being composed of a number of synchronously diving groups. Within such groups one can sometimes recognize small "subgroups" of a few (2 to perhaps 12) animals that are often seen together, regardless of the group or school composition around them.

DISTRIBUTION

Marine mammal collectors of the Sea Life Park, an Hawaiian oceanarium, suggested that spinner dolphins occur habitually at certain areas along the island shores, while they are largely or wholly

³An Atlantic Research Corporation LC 32 hydrophone, a Hewlett-Packard 466A preamplifier, and a Uher 4000s ¼-in tape recorder composed the recording gear. The upper frequency response of this system was approximately 20 kHz at 7½ ips.

absent from others. This led us to collect sighting and capture locations for the entire Hawaiian chain. The same collectors reported that after collection of animals from a given school, the school as a whole might become shy of the boat for an indefinite period, and suggested that it occupied a given area of coast and the school might have integrity through time.

We found that spinner dolphins occur throughout the Hawaiian chain, from its northwest-most limit at Kure Atoll (lat. 25°40' N, long. 175°38' W) to its southernmost limit at South Point, or Ka Lae, on the island of Hawaii (lat. 18°49' N, long. 155°41' W). Occurrence is not random, but spinner dolphins are gathered in small to moderate schools (6 to about 250 animals) near all major islands and shoal areas and can be found with some regularity near certain shoals or coves. Only near small islands that drop abruptly without having significant shoals, such as at Nihoa Island, have we not found spinner dolphins. The following

is a synopsis of known spinner distribution. Unless otherwise specified, all sightings were by the authors. Specific records are shown in Figure 3.

Kure Atoll. On 3 September, 1971, Norris visited Kure Atoll. The commanding officer, Lt. (j.g.) Joel Greenberg, reported having seen a school of 20-30 spinner dolphins enter a west pass into the atoll lagoon. Without prompting he described their spinning behavior.

Midway Island. On the midafternoon of 3 September 1971, a school of approximately 35 spinner dolphins was noted in shallow water at the edge of the channel inside of Eastern Island. The regular daytime occurrence of animals in the shallow atoll lagoon was reported to us by residents of Midway.

French Frigate Shoals. On 12 September 1971, at 0830 h, 30 animals were noted just off Shark Island, spinning and leaping.

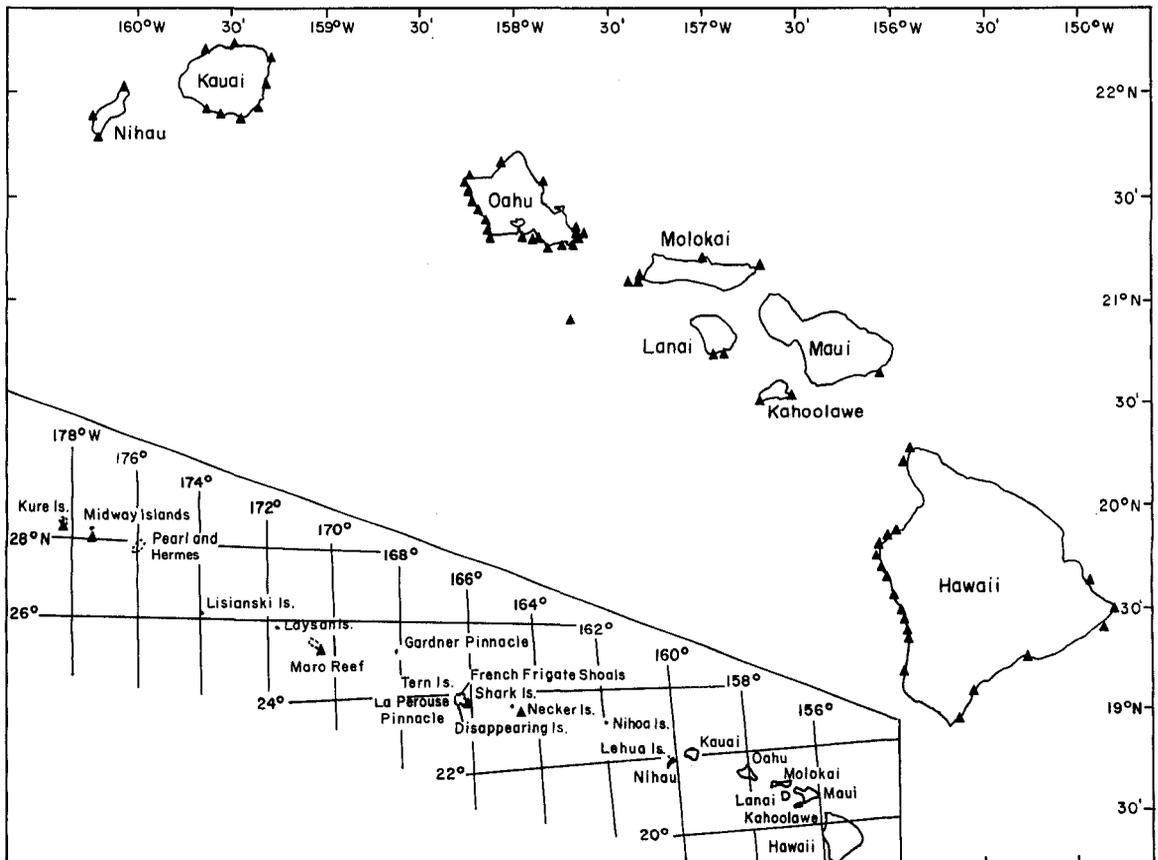


FIGURE 3.—Sightings of spinner dolphin schools by the authors (triangles) in the Hawaiian Island chain.

Pearl and Hermes Reef. Edward Shallenberger reported seeing a spinner dolphin school at this location in the fall of 1978, entering the central lagoon during the day.

Necker Island. On 13 September 1971, 10.2 mi east-southeast of Necker Island at 1600 h, a school of about 30 spinner dolphins was seen.

The following localities in the northwest Hawaiian chain were visited without seeing spinner dolphins; Salmon Bank, Lisianski Island, Laysan Island, Gardner Pinnacles, and Nihoa Island. Five to 10 animals that may have been spinner dolphins were seen 18.5 mi, 134° T from the wreck at Maro Reef, by Ens. Albert Sarra, U.S. Coast Guard, on 9 September 1971.

Niihau Island. Spinner dolphins have been sighted at Kaumuhonu Bay (60 + animals) at the southwest tip of the island, between Lehua Island and Kikepa Point (20 + animals); smaller schools (15 + each) have been noted along the southeast shore near Pueo Point and on the northwest shore at Nonopapa. The Nonopapa record was of a traveling school that moved close to shore along perhaps half of the northwestern coast.

Kauai Island. Spinner dolphin schools were found around Kauai Island at 3-16 km intervals, except along its western coast. The largest schools were estimated at 150 animals on the Napali coast, a 70-80 animal school just north of Kahala Point, and an estimated 60 animal school between Hanapepe and Kaumakani. Smaller schools, scattered along the south and east coasts, averaged about 15-30 animals. The only obvious difference between the vacant coast and the occupied areas is that vacant areas have much narrower, shallow water shelves devoid of deep indentations in the coastline.

Oahu Island. Records from the various sources over 14 yr (1962-76) show that two broad areas of the coast are nearly always occupied by spinner dolphin schools during the day. First, along the Waianae coast between Barber's Point and the vicinity of Kaena Point (the west or Kona shore), schools estimated between 30 and 100 animals can nearly always be found close to shore during the day. Second, an apparently larger school or schools is often seen in the coastal area between about Pearl Harbor and Makapuu Point. Schools of ani-

mals seen in this area have been estimated to number from 40 to 250 individuals. Small schools have been seen near Kahana Bay and Waimea Bay. Because this is the windward coast, subject to almost constant tradewinds, little collecting effort has been expended there and dolphins may be more common than our records indicate. A relatively narrow shelf (1.6 km) exists along the Waianae coast except at Kaena and Barber's Points where it broadens considerably. The shelf around the remainder of the island is much broader, averaging about 4 km, and is marked on the northwest and northeastern coasts by a fringing reef.

Molokai-Lanai-Kahoolawe-Maui. Geologically this four-island complex has resulted from one series of volcanic eruptions, producing islands with interconnecting shallow areas and channels. Spinner schools have been seen at several locations around the margins of this complex, but seem rather seldom to travel to inshore locations over extensive shallow areas such as that at Lahaina Roads (Auau Channel) or over the flats between Molokai and Lanai Islands (Kalohi Channel). Dolphin schools in such areas would have to travel 11 km or more from deep water to reach these shorelines.

Large spinner schools have been seen over Penguin Bank (between western Molokai and Lanai Islands), the south coast of Lanai, especially near Manele Bay (40-100 animals), and along the south shore of Kahoolawe, especially near Halona Point; small schools were seen on the north Molokai shore at Kalaupapa and Cape Halawa, along the Hana coast of Maui, and at Lipoa Point on the northwest end of Maui. Two records of spinner dolphins accompanying humpback whales near Lahaina were reported to us. The bottlenose dolphin, *Tursiops* sp., has often been seen with these whales.

Hawaii Island. Spinner dolphin schools have been found at scattered locations around the entire periphery of the island except for the northeast shore, though there are some shorter stretches of coast where we have never seen schools. It is not surprising, in view of the large size of this island, that there are more localities of regular occupancy by porpoise schools than for any other island. We found seven areas of regular occupancy and four localities with more transient occupancy.

On the lee side of Hawaii, the largest school was centered at Keahole Point, ranging along about 23 km of coast, from Honokohau Harbor to Kiholo Bay. In all, there are estimated to be about 200-250 animals generally occurring in this area, and they may be found in a single school at times or fragmented into two or three smaller schools, separated by a few kilometers of coastline. Here, the dolphins do not seem to occupy any of the small coves consistently, but to congregate over the rather extensive area of shallow water, moving back and forth. Not uncommonly, parts of this aggregation moved during the day beyond the limits listed above and may move as far as Kailua-Kona or beyond, though the constant sea traffic in that harbor seems to prevent normal daily quiescence (defined below). We have termed these animals collectively the "North Kona School." Twenty-eight kilometers to the south, at Kealakekua Bay, a school ranging from 2 to 70 animals (average 25 animals over 73 observations) was found. In our observations, dolphins occurred in this bay on 74% of 113 observation days. They most commonly occupied the deeply indented bay but sometimes were found on the shallow area north of the bay to Keauhou or occasionally nearly to Kailua-Kona. Less commonly they were found to the south in or near the very small bays at Honaunau (City of Refuge) or Hookena.

The entire 56 km stretch from Hookena to South Point seems not to harbor spinner dolphin schools on a regular basis, though it should be noted that a military air closure zone prevented our flying over the Milolii area regularly. We have a single record of a 20 animal school at Milolii. This precipitous coast drops abruptly into deep water, without shallow areas alongshore. Much of the coast is composed of relatively new lava flows from nearby Mauna Loa volcano.

Small schools, estimated generally at about 20 animals, were seen, usually in very rough water, at South Point, between Ka Lae and Honuapo, over the modestly developed shallow area there, or occasionally in the deep cove at Kaalualu.

At Keauhou Cove, directly below Kilauea Crater, a small school (20-25 animals) was consistently found. The dolphins came into very shallow water there in an area protected by Keaoi Islet and flanking coral heads, which produce a small area of calm water along an otherwise rough water coast.

Cape Kumukahi, the easternmost point on the

island, hosted a population of about 30 animals. Several small irregular bays along the southern edge of the cape form the "home bay" in this area, with animals being noted at times as far as Opilukao Cove.

The largest school on the windward shore (ca. 100 animals) was often found at Kaloli Point, 18 km south of Hilo Bay. This location seemed also to be the northernmost area of occupancy on this side of the island. The dolphins were typically found in the bay protected by the point and fringing coral reefs. The rather shallow bay (maximum depth 20 m) is close to deep water to the south.

The 112 km stretch of coast from Kaloli Point to the north end of the island (Upolu Point) seemed devoid of resident spinner dolphin schools. It is also the site of the major sugar cane processing plants on the island. Effluent from these plants seems to produce murky waters along the coast and clearly contributes to the long drift lines of flotsam from processed sugar cane. Whether the absence of animals and this activity are related is unknown.

At the north tip of Hawaii we occasionally saw or heard of small schools of spinner dolphins (10-30 animals) in the area between Kawaihae Bay and Honoipu, though more often the entire stretch of coast was found to be without animals from the Kiholo Bay to the north tip at Upolu Point. This circumstance is anomalous, in that well-developed, shallow-water areas occur along this shore, where schools might come during the day, and where the sea is generally calm.

REST AREAS

Three features of the distribution of spinner dolphins in the Hawaiian chain stand out. First, the distribution is discontinuous. Some coasts may have several areas where dolphins congregate, and others may have stretches of many kilometers in extent where no animals are seen. Second, certain coves or shallow areas are clearly regular aggregation sites, while others seem to be used much more infrequently. Third, some areas consistently carry more animals than others. As we will demonstrate, spinner dolphins come inshore during daylight hours to enter a quiescent period of some hours duration, and we think of these congregation sites alongshore as "rest areas."

What typifies such rest areas? First, all rest areas are shallow sandy areas with <50 m depth over part of their extent. They are usually com-

posed of a mixture of open sandy bottom dotted with coral formations. Coves may or may not be present. All rest areas are close to deep water. Usually water >500 m depth can be reached within a few kilometers. Some schools, such as those in the Waikiki (Oahu) or Manele Bay (Lanai) areas, have access to considerably shallower water than others. Schools living there may be restricted to waters no deeper than about 600 m since our observations on the Kona coast of Hawaii indicate that schools do not move more than a few kilometers from shore at night. Other schools, such as at Keahole Point (Hawaii) regularly move into water >2,000 m depth. Of course, the observations we have made on the island of Hawaii may not hold elsewhere.

Apparently spinner dolphins only occasionally travel onto extensive shallow areas like that at Lahaina Roads (Auau Channel), which is about 24 km long. Instead they typically congregate along its margins, along the south shore of Lanai Island and Kahoolawe Island, where deep water is nearby. The areas most closely studied here are Kealakakua Bay and Keahole Point, both have deep water accessible within 1.5-2.5 km of shore. The inference is that rest areas are chosen by dolphins not only for physical characteristics such as depth, bottom type, and perhaps calm water but also for their accessibility to nighttime feeding areas.

Spinner dolphin schools also rest in atoll lagoons. At Kwajalein Atoll, on 10 September 1973, at 1630, a school of about 40 spinner dolphins was noted about 1 km inside Bigej Pass. The school was moving toward the pass, presumably on its way out to sea. A local resident told us that the school was regularly in this pass and not found in other nearby passes into the central lagoon. Similar observations have been made at Kure Atoll, Midway Atoll, and near Shark Island at French Frigate Shoals. The animals (approximately 35), resting quietly in a shallow channel not far inside Eastern Island at Midway, were sighted from a helicopter. Probably wherever atolls and spinner dolphins occur together the animals use the atoll lagoons for rest.

In the eastern tropical Pacific a large spinner dolphin population occupies oceanic areas far from land. In view of the use of shore situations elsewhere in the range of the species, one wonders what, if any, substitution is made. Norris and Dohl (in press) have speculated that the frequently observed association between spinner and spotted

dolphins in the eastern tropical Pacific (this association does not occur in Hawaii) may hold the answer. Spinner dolphins may seek the schools of spotted dolphins for refuge during rest in the open sea. We believe this may be true because spotted dolphins feed during the day, while spinners are nocturnal feeders, and spinner dolphin schools have been observed to join spotted dolphin schools in the morning (Norris et al.⁴). If such rest association occurs, the spinner dolphins are associating with alert animals in this oceanic area. Related to this the yellowfin tuna seine fishermen chase and encircle dolphins to catch tuna, most fish apparently follow the spotted dolphins. Since the association between tuna and dolphin is probably food based, the tuna may be following the dolphin species that is actively searching for food. That is, like the tuna, the spinner dolphin may follow active dolphin schools.

Spinner dolphins resting along shores maintain a continuous but slow locomotion, and it seems likely that the searching or feeding activities of spotted dolphins would not greatly change these requirements for rest.

MARKED ANIMAL STUDIES

Dolphin schools are seen frequently at the same localities while other areas never seem to harbor them. Are these schools of resident animals, or are they composed of transients that for some reason choose certain regions of the coast for rest? The frequent observation of dolphin collectors that a given school will avoid their vessel after animals have been collected from it (Norris and Prescott 1961) indicates possible residency. On the other hand, dolphin schools are not always in these rest localities, and the number of animals using a given cove may vary widely from day to day. This indicates fluidity in school structure and variability of school movement. Such fluidity has been noted for other porpoise schools by Würsig and Würsig (1977) and Saayman and Tayler (1979).

Because we were concerned that the spinner dolphins of the Kona coast of Hawaii should not fear our vessel, we sought to recognize individuals by natural scars and marks rather than by placement of tags. Ultimately we were able to catalog 50 recognizable individuals and resight-

⁴Norris, K. S., W. E. Stuntz, and W. Rogers. 1978. The behavior of porpoises and tuna in the eastern tropical Pacific yellowfin tuna industry-preliminary studies. Natl. Tech. Inf. Serv., Final Rep. No. MMC76/12 PB 283-970, xi + 86 p.

ings provided a partial picture of the school and individual movements. Our shipboard work with dolphin schools was restricted almost wholly to Kealakekua Bay through most of 1970. Only toward the end of that year and during 1971 and to a limited extent later, much sea time was spent in other areas. Hence a large proportion of our sightings do not bear on the question of dispersal distances or rates by individual dolphins. We gathered no information on possible interisland movements.

By far the most useful scars and marks were those of the dorsal fin. Twelve of our animals were in this category (Figure 4). These animals could be resighted from shipboard, and sometimes from considerable distances. It is not surprising that 49, (64%) of our 76 resightings were of these animals.

Many marked animals had scars or pattern peculiarities. Such marks could only be sighted on dolphins at the bow of the observation vessel, or from our MOC. The MOC was used sparingly because it was noisy and disturbed dolphin schools and because it was safe only in calm seas. Thus, information on repeated social associations within

schools is limited to two sets of sightings and journal notes over 14 days, all within Kealakekua Bay. In any school only a few individuals swam at the bow of a vessel, while others stayed well clear, thus reducing the chances of sighting many animals. Of 38 animals cataloged with body scars or marks, there were 27 resightings. The final marked animal recorded was an individual with a vertical white stripe on its dorsal fin (Figure 4).

Our store of recognizable animals built up slowly over the entire period of the study, thus making interpretation of movements difficult; nonetheless, some important ideas emerge: 1) No resident school permanently and regularly uses a given cove or local region of shoreline. Instead, each cove or resting spot may harbor a given subgroup of dolphins for a matter of days or weeks. 2) Schools are labile mixtures of groups and subgroups. 3) Individual movements may span the entire Kona coast, or even beyond (true ranges of movement remain unknown). A few "marked" individuals have been seen over rather long periods, but other equally recognizable animals have been seen only briefly, or never again



FIGURE 4.—Spinner dolphin with vertical white stripe on both sides of its dorsal fin. We suspect that this animal had shed a radio pack after the pin had migrated out of the fin.

after an initial sighting, suggesting either rapid population turnover or high levels of intermixing between the various schools of the area.

Two pale animals were seen. They were very different visually from their associates. This was especially evident from the air. They were seen along the entire southern Kona coast from Keahole Point to Kamilo Point east of Ka Lae (South Point) and over the longest time span for any "marked" animals (1,220 days out of the total 1,246-day recording period). These pale animals were seen either alone or on occasion together in the same school. These data are suggestive only, because such pale coloration cannot be assigned definitely to a given animal since it is a recurrent condition in the species. For example, such a pale animal was captured near Oahu, and for some years was an exhibit animal at the oceanarium, Sea Life Park. The animal, called "haole" for "white person", gradually grew darker during captivity but always remained slightly pale. Per-rin (1972) described a pale animal from the eastern tropical Pacific, as "albinistic."

Let us examine each of our conclusions in turn. First, is the question of residency. Taking only those animals recognizable from the surface, we find that 7 of 12 animals were seen in both the large Keahole Point schools and in the smaller Kealakekua Bay schools. The pale animals were seen both in Kealakekua Bay and Keahole Point schools and far to the south at Kamilo Point. There were long periods when a given animal was not seen at one or another locality. This information cannot be usefully quantified because schools were sometimes large and all animals could not be examined and because our records are not the result of concerted attempts to check each animal in a given school. Instead, the records reflect opportunistic sightings during the pursuit of other activities.

Animals clearly moved back and forth between the Keahole Point and Kealakekua Bay assemblages. Of the 12 animals, 6 were seen at more than one locality and then returned to the first locality of sighting at least once. Three animals were seen at a single locality only, but this may reflect low sighting frequency rather than lack of movement.

Finally, three animals were seen at two or more localities but did not return to the locality of first sighting. For these reasons we reject the idea of a given cove having a definable resident school (Table 1).

TABLE 1.—Movement of Hawaiian spinner dolphins that were identified by natural scars and marks.

Dolphin number	Total time observed (days)	Maximum distance travelled (km)	Number of sightings
1	293	18	3
23	183	0	3
24	1,096	36	14
30	342	36	11
32	246	0	3
39	236	36	3
40	275	36	4
44	170	36	6
45	1,220	113	7
46	862	10	3
49	39	36	2
50	1	0	1

Reversals = 6

One location = 3

Two or more sequential locations = 3

Our data are too incomplete to show how long a given animal might spend at a single locality, or how often it switches between rest localities. Only the number of consecutive days during which a given surface-visible marked animal was seen at a single locality vs. the number of days of consecutive observation during the sighting period is indicative. Considering the animals for which most resightings are available: numbers 24 and 30, during four separate continuous periods of observation of 9, 8, 9, and 10 days, animal 24 was seen 2, 2, and 3 days consecutively (Table 2). Animal 30 was seen only once, 2 days in a row, during consecutive observation periods of 7, 10, and 10 observation days. Animal number 13 (a large calf traveling with its mother) was seen three consecutive days during a 16-day observation period at Kealakekua Bay. During consecutive observation periods in which the observer moved from Kealakekua Bay to Keahole Point, certain animals were noted on consecutive days at the two localities, indicating a switch in a single night from one to the other. These data indicate that movements are frequent, at least between the Kealakekua Bay and Keahole Point rest areas.

As for the conclusion that dolphin schools consist of labile aggregations of groups and sub-groups, the best information comes from fluctuations in school sizes with which a given marked animal was associated. The results reflect almost

TABLE 2.—Occurrence of a single spinner dolphin (No. 24) and the size of schools in which it was seen at Kealakekua Bay, Hawaii, 1970.

Dates of observation	Estimated school sizes	Number of times seen
28 Apr.-6 May	15-30	3 days of 9
23 June-30 June	15-40	2 days of 8
10 Sept.-18 Sept.	25-36	3 days of 9
28 Oct.-6 Nov.	7-120	3 days of 10

the entire range of school sizes observed. For example, at various times number 24 was found in schools varying from 7-10 to 120 animals, and number 30 covered about the same school size range, from 6 to 150 animals. Observations from the MOC showed that on one occasion the same subgroup, with the same general internal arrangement of animals, persisted for at least 3 days. Many times, during three consecutive observation days (25-27 March 1970) the same subgroup of five animals came to the bow of the MOC. This sort of association is well known in captive schools and persists for long periods of time (McBride and Hebb 1948; Tavolga and Essapian 1957; and Bateson⁵). Such groups in captivity may be constructed of related or nonrelated animals or even of animals of different species (Bateson see footnote 5). Thus, while our observations of wild schools do not provide proof, we expect that some subgroup structure may persist over long periods and that familial lineages may be important, as has been observed in captivity (Tavolga and Essapian 1957).

The role of subgroups in larger dolphin schools is apparently not simple. Such schools are not simply composed of groups and subgroups that themselves have cohesion. Instead, there are also some assemblages that seem typical only of large schools. For example, in large schools, groups are often segregated. Groups of juvenile animals or of mother-young pairs may be seen. Large schools differ from one another by the presence or absence of such groups. Some schools were composed only of adults, while others had a high proportion of young animals. Subgroups may move between schools. Some social ordering, largely related to growth and reproduction, may take place in schools regardless of the origins of their constituent parts. A major force in such ordering within large schools may be the aggression of certain large adults, that may be either male or female, who herd vulnerable groups to central locations within the school (McBride and Hebb 1948). Such patterns have been proposed for *S. coeruleoalba* by Kasuya (1972) and for *S. attenuata* by Kasuya et al. (1974).

AERIAL BEHAVIOR PATTERNS

An experienced observer of spinner dolphins can

quickly judge the activity state of a school by watching its aerial patterns. It is possible to judge the alertness of school members by checking the kind and frequency of aerial patterns. In fact, such analysis soon makes it obvious that the entire sequence of changing behavior patterns through any 24-h cycle is related to the level of activity, or "emotional state," as indicated by aerial patterns.

Spinner dolphins not only "spin" but perform several other clearly recognizable aerial patterns. These include leaps, tail-over-head leaps, backslaps, headslaps, noseouts, and tailslaps, or a combination of these patterns—each performed with variable vigor and frequency at various times of day.

The spin. The spinner dolphin rushes to the surface as if about to make an arcing leap, and at the last instant, when most of its body is out of water, tips its flukes slightly and flexes its tail stock, causing the airborne animal to spin about its longitudinal axis. As many as four revolutions may be made in the course of such a leap (Hester et al. 1963). The dolphin may literally appear to flicker as flippers, flukes, and the dorsal fin flash by. The animal falls back into the water, usually partly on its side, and its rapidly rotating body scoops out a hollow of water around the sinking animal. The hollow then collapses producing a welter of spray (Figure 5) and a discernible clap of sound. The spin is enhanced in air by postural movements, in addition to the momentum initially imparted when leaving the water. Just as a gymnast flexes his or her body or as a skater moves elbows in a spin, the spinning dolphin flexes its head and tail and moves its flippers toward or away from its body (Figure 6).

Spins are usually performed in a series of descending intensity (as are other aerial patterns). A given animal may spin as many as a dozen times in succession, each successive spin generally being of somewhat reduced intensity compared with the last. The first leap may reach an apex perhaps 3 m above the surface, while in the last of a series the animal may not clear the water at all. Most spin series are short, being composed of three or four spins.

All age-classes spin. It is not uncommon to see small calves spinning repeatedly in moving schools. In one case a young animal leaped into a spin while in a feeding school, landing a dozen meters off our bow. Each successive spin brought the animal closer to us, as it was seemingly obli-

⁵Bateson, G. 1965. The cetacean community in Whaler's Cove-Sea Life Park.

FIGURE 5.—Spinner dolphin reentering the water after a spin, seen from below. Note the longitudinal hollow of water scooped out by the rotating animal. Photo by Henry Groskinsky, courtesy Time, Inc.

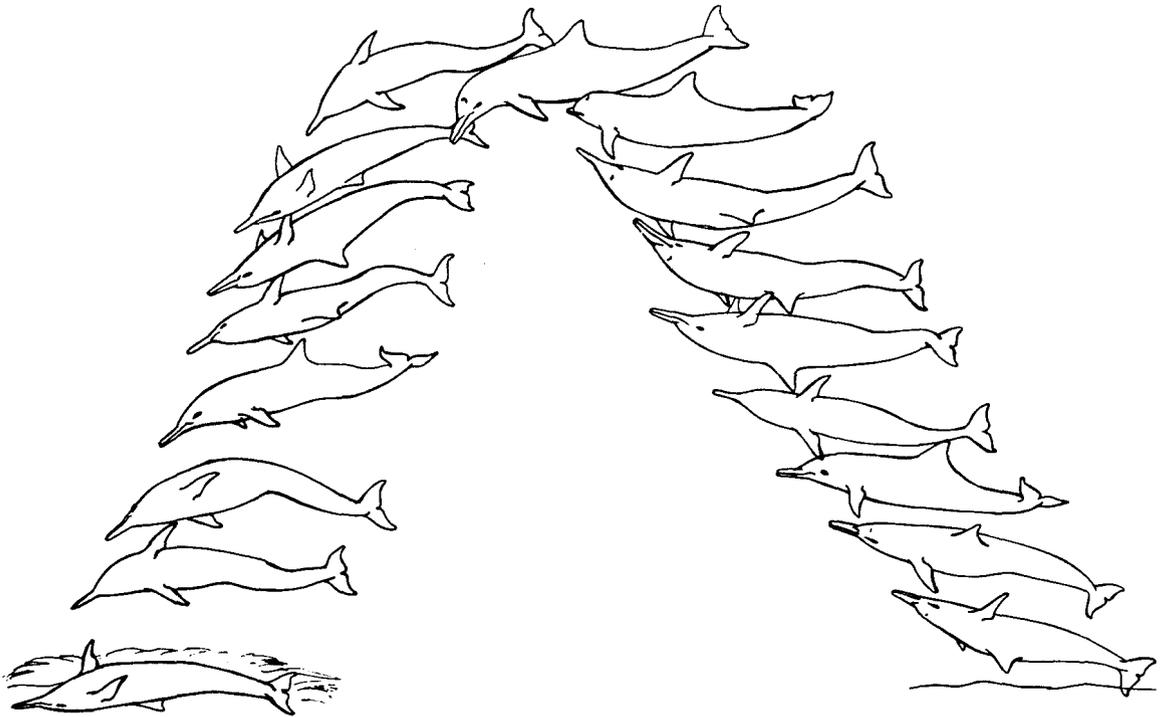
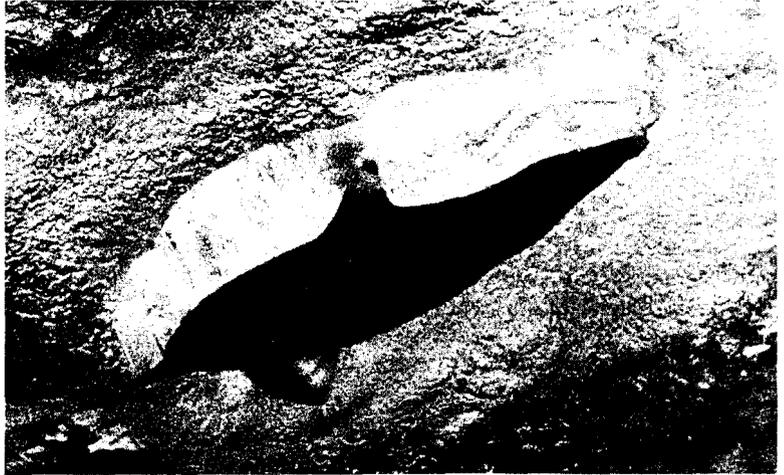


FIGURE 6.—Body postures of spinner dolphins during a spin. Vertical and horizontal dimensions of leap not to scale. Redrawn from Hester et al. (1963).

ous of our presence. The last spin launched the animal nearly at the bow; it fell back into the ship's bow wave, startled, and swam rapidly away below the surface.

Spins may be seen in all parts of a school. Leadership or dominance do not seem to be the obvious factors in spinning behavior. In fact, the opposite could be true since very young animals spin, and

in our observations of captive spinner dolphins a high frequency of spinning was observed in an animal that had not been socially accepted into the resident captive school. The best correlation of frequency of spinning and the condition of a school seem to relate to alertness, or activity level of the animals involved, the greater the alertness the more frequent the spins. The more spread out a

school the more frequent spins seem to be. In feeding schools, which are the most dispersed of all school formations, spinning and other high energy aerial behavior occur almost continuously.

The leap. The most common aerial behavior in which spinner dolphins actually leave the water is the leap. Spinner dolphins perform leaps by bursting from the water at about a 30° angle, rising a meter or two above the surface, and falling back into the water on the belly or side in a welter of foam. Less frequently, reentry may be made cleanly, snout first.

Tail-over-head leap. The most active and perhaps physically demanding aerial behavior pattern is the tail-over-head leap and its variant, the tail-over-head leap with spin. These aerial patterns are seen only when the Spinner dolphin school is most active. In this pattern the animal bursts from the water at a rather high angle, slings its tail over its head in a wide arc, usually trailing a spiral of spray and enters tail first, often slapping its flukes against the water with a loud "thwack" in the process (Figure 7). On occasion this may be accompanied by one or two revolutions of a spin at the same time.

Backslap. The animal leaps about half or a little more of its length out of water at about a 30°-45° angle, upside down. As it falls back, it arches its body sharply, giving the water a sharp slap with the dorsal surface of its head and beak (Figure 8). Backslaps are often performed in slowly moving schools.

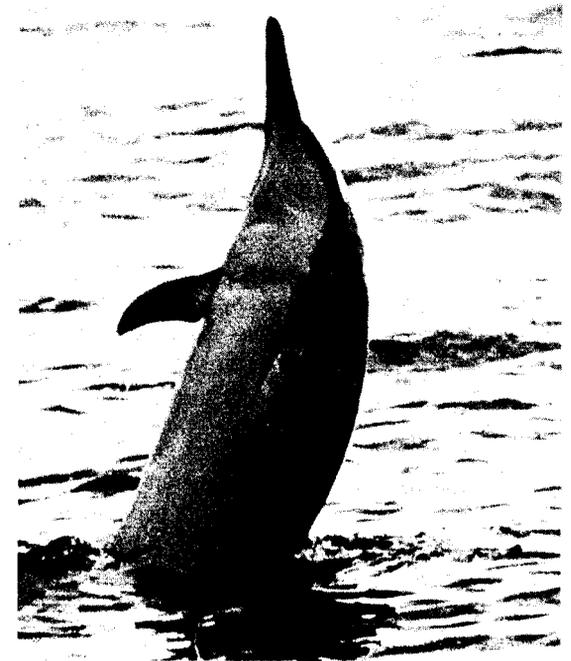


FIGURE 8.—A typical backslap of a spinner dolphin. As the school moves slowly the dolphin emerges in the direction of swimming, belly up, and arches its back at the last instant and slaps its back against the water.

Headslap. The reverse of the backslap. The animal emerges in the normal position, once again at about 30°-45° angle to the water surface, and then flexes its head sharply downward, slapping its chin and lower beak against the water (Figure 9). It is one of the most common patterns seen in moving schools.

FIGURE 7.—The tail-over-head leap of a spinner dolphin. This may, at times, be combined with a spin.

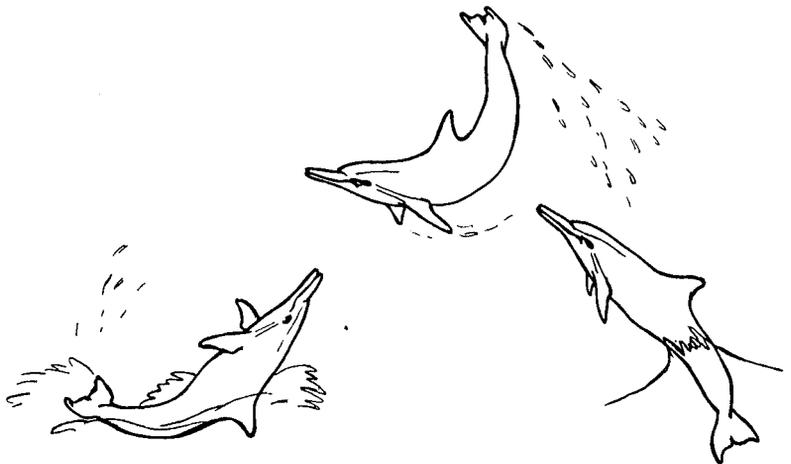
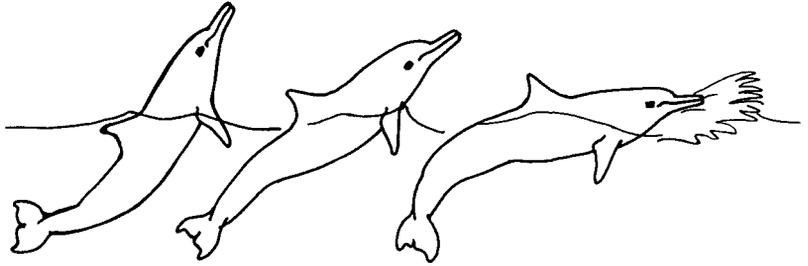


FIGURE 9.—A headslap. The spinner dolphin emerges belly down in the direction of swimming and flexes its body forward sharply at reentry.



Noseout. The least active aerial behavior. The spinner dolphin simply arches its back as it swims to the surface, raising its snout into the air. It is sometimes seen briefly when a resting school is disturbed, or in schools where other, more active behavior is occurring. It is often the first aerial behavior seen in an awakening school.

Tailslap. This pattern may be performed in either the normal or the inverted position. With the dolphin at the surface the tail is arched, bringing the flukes above the surface. The flukes are then brought down smartly against the water producing a clearly audible sound. In the inverted position an animal may sometimes scull along making repeated and rapid tail slaps in a behavior we have called "motorboating," because it not only leaves a continuous wake, but makes a "pop pop pop" sound. An animal may slap 10 to 20 or more times in succession in this way (Figure 10). A whaler's term, "lobtailing," describes the same behavior, but seems less descriptive than "tailslap," a term now widely used by porpoise trainers.

What are the functions of aerial behavior? A key point, we feel, is that each pattern, with the possible exception of the noseout, clearly makes noise and, in fact, seems primarily structured to make noise. For example, in a headslap the last compo-

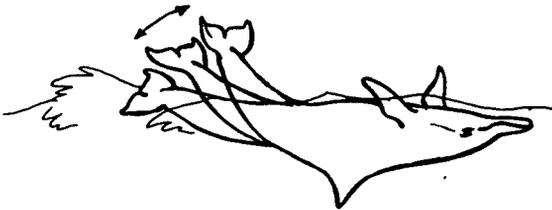


FIGURE 10.—An inverted tailslap by a spinner dolphin. Tailslaps also may be made in normal body posture. Often a series of a dozen or more slaps may be made at a single time, which has been termed "motorboating" because of the white wake and the sound produced.

nent of the pattern is a rapid flexure of the trunk and neck causing the chin and throat to slap against the water. The tail-over-head leap effectively slaps the flukes against the water with great force. The spin scoops a cavity from the sea surface whose walls collapse and thus produce a sound we have heard both above and below the water. Other aerial patterns are similarly structured. Such sounds probably radiate in all directions. Dolphin sound generation and beaming apparatus, on the other hand, transmits sound in a structured beam, directed forward (Schevill and Watkins 1966; Norris and Evans 1967; Evans 1973). This beaming is better known for clicks than whistles or burst pulse signals, though apparently also true of the latter, at least in the killer whale, *Orcinus orca* (Schevill and Watkins 1966). The directionality of clicks has been discussed for *S. longirostris* by Watkins and Schevill (1974). Thus, while vocal signals are directed almost wholly in certain sectors, the sounds of aerial behavior are likely to approach omnidirectionality. Our recordings indicate that none of the signals of aerial behavior propagate long distances. Tail slaps may be the loudest.

Aerial behavior is most frequent in fully active schools in which the animals are dispersed, sometimes rather widely. In tight resting schools (see below) sounds of all kinds except for desultory clicking are nearly absent. Conversely, our observations of a captive spinner dolphin school held in a community tank at the Oceanic Institute, Oahu, Hawaii, showed that aerial behavior continued through the night and, in fact, was most frequent in the dark. Thus, high frequencies of aerial behavior seem correlated with conditions in which many animals in the spread school cannot see each other.

Finally, these patterns are stereotyped by species, and a trained observer can often visually identify the genera or species of dolphins by their aerial patterns, sometimes from long distances.

Perhaps the dolphins can make such identifications underwater by sound.

What can the use be of such sound signals? The following possibilities seem apparent: 1) If we can gage the activity state of a school by its aerial behavior, it is likely that the dolphins can do so too, and probably in a more refined way than we can; 2) such sound signals may be used where vision is useless; 3) school cohesiveness in the dark; or when animals are spread beyond the limits of vision, may be promoted by repeated short-range omnidirectional sound signals from all parts of a school. The incidence of aerial behavior is correlated with times when such signals would be most useful. This seems to us to be the most likely function.

We considered, and rejected the idea, that the spin might be a pattern relating to dominance or courtship in the school. This seems refuted because animals of all age classes and both sexes spin and because captive observations have shown that even animals that have been rejected from the social structure of a school spin.

Another possibility is that spinning is related to removal of ectoparasites such as remoras and copepods. While it might be useful occasionally in detaching such creatures, we have never seen a case in which this seemed to be occurring, and essentially every animal observed to spin was apparently without parasites. Captives spin regularly even though free of parasites.

THE DAILY ACTIVITY CYCLE

Observations of spinner dolphin schools along the Kona coast of the island of Hawaii, and to a

minor extent elsewhere in the Hawaiian chain, show a regular sequence of activities during each 24-h period. Broadly, this consists of nighttime feeding, about which we know little, morning coastward movement that brings the animals into coves and sheltered coastline areas, rest, awakening, zigzag swimming, and then departure to the feeding grounds. Each of these activities will be discussed in turn.

Feeding

Feeding is upon scattering-layer organisms (Table 3) and seems to be performed during synchronous or subsynchronous dives of large and dispersed schools. What we take to be feeding dives start as early as dusk, before most of the scattering layer approaches the surface, and such evidence as we have (mainly from a single radiotracking, from chance encounters with schools at night, and from schools that we have followed to the feeding grounds) suggests that the schools patrol along the breaks in the submarine island slope and toward morning gradually make their way into shallow water over the shelf. A radiotracked animal, caught over approximately 140 m of water at Keahole Point just before dusk (at 1650 h) on 1 March 1971, moved back and forth along the shore between a point near Kailua-Kona and Kiholo Point. A detailed radiotrack was made during the night of 1-2 April (Figure 11). The animal stayed with a large school that moved slowly offshore and by 2000 was over the island slope. The group then patrolled back and forth over the slope within a stretch of coast approximately 20 km in length and over water that varied from about 360

TABLE 3.—Squid and shrimp in the diet of Hawaiian spinner dolphins.

Sample and date	Capture locality	Squid	Shrimp
0170-42 Sept. 24, 1970	1 km off Ala Wai, Oahu	28 mantles (mantle length 25-52 mm, mean 38.9 mm) 5 <i>Abralia astrosticta</i> 14 <i>Abralia trigonura</i> 67 squid beaks, probably of the same species	11 pasiphaeids (to 17.8 mm carapace length) 1 small 4 abdominal portions 1 caridean cephalothorax Probable euphausiid fragments No identifiable remains
0170-35 Mar. 25, 1970	Off Waikiki, Oahu	2 <i>Abralia astrosticta</i> 7 <i>Abralia trigonura</i> 152 squid beaks of the above species 49 macerated squid	
0171-1 Jan. 8, 1971	200 m off Kailua-Kona Harbor, Hawaii	2 <i>Abralia astrosticta</i> 6 <i>Abralia trigonura</i> 204 squid beaks, probably of the above species 1 <i>Histioteuthis</i> sp.	20 <i>Sergia fulgens</i> (12.5-15.5 mm carapace length, mean 14.6 mm)
0171-2 Jan. 8, 1971	200 m off Kailua-Kona Harbor, Hawaii	2 <i>Abralia astrosticta</i> 8 <i>Abralia trigonura</i> 310 squid beaks of the above species	1 <i>Acanthephyra</i> sp. 1 <i>Pasiphaea</i> sp. 2 <i>Pasiphaea</i> sp. 15 <i>Sergia fulgens</i> (12-14.5 mm mean 13.6 mm. Some of the above may be of undetermined species) 1 <i>Oplophorus grimaldii</i> (identification probable) 3 <i>Acanthephyra</i> sp. (identification probable)

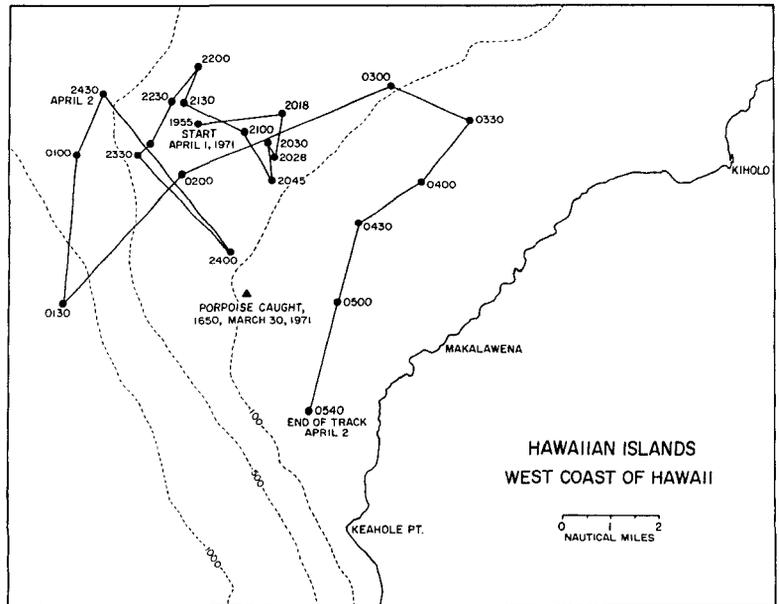


FIGURE 11.—Radiotracking chart of a marked spinner dolphin, 31 March-2 April 1971. Dolphin stayed in moving school of 100 animals presumably feeding over the island's submarine slopes.

to 2,600 m deep. By 0300 the school and the radiotagged animal had moved closer to shore and continued to move in ever shallower water until dawn.

Feeding schools were observed on three occasions at dusk. Each was composed of widely scattered groups, covering as much as 3 km in widest dimension, moving together. Diving was subsynchronous. Before a dive occurred, groups were evident and there was much aerial behavior across the entire width of the school. Then groups of the school dove individually, all following within approximately a minute or two. Dives were long, averaging 3.5 min according to our records. Surfacing was approximately as coordinated as diving; that is, the various groups straggled to the surface over a minute or two.

It was striking to see these very broad diffuse schools reverse their course in relative synchrony (within a minute or two), even at dusk, indicating a communication mechanism, probably acoustic, that could pass information rather quickly across the school.

Stomach contents were obtained from four spinner dolphins caught early in the day (before noon), while three animals taken in the afternoon had empty stomachs. This same pattern seems to occur in the oceanic spinner dolphins of the tropical Pacific, and a high percentage (65.3%) of empty stomachs (not segregated according to time of day) from 49 spinner dolphins taken from the eastern

tropical Pacific were empty (Perrin et al. 1973). A time-stratified sample would probably show some food in the stomachs in the morning before digestion of the night's catch is complete, with empty stomachs in the afternoon. If spinner dolphins were diurnal feeders, one would expect few empty stomachs during the day at any time. The observed morning defecation period also fits this scheme. We conclude from our own observational data that the spinner dolphin in the open eastern tropical Pacific and around the Hawaiian Islands feeds at night. Our evidence, and that from other studies, suggests that it feeds upon scattering-layer organisms found at considerable depth. Fitch and Brownell (1968) reach a similar conclusion from otolith studies of stomach contents of five spinner dolphins taken from the yellowfin tuna grounds; they stated: "We feel certain that three of the cetaceans we investigated (*Kogia simus*, *Stenella longirostris*, and *Lissodephis borealis*) had been feeding 800 ft (250 m) or more beneath the surface . . ." Perrin et al. (1973) similarly concluded that spinner dolphins are feeding mostly on mesopelagic fish and squid, with a small increment of epipelagic squid species in their diet. Our results (Table 3) confirm these earlier works, but show a considerable component of sergestid crustaceans in the diet of the Hawaiian spinner dolphin. Epipelagic squid were absent, though common in Hawaiian waters, while such relatively deepwater forms as *Abralia astrostricta*

and *A. trigonura* were common in the stomach samples but rare in collections of squid from Hawaiian waters. Richard Young⁶ described *A. trigonura* as being uncommonly taken in Hawaii, but being a vertical migrant occurring from 500 m depth during the day to the upper 100 m at night. This species made up the majority of our samples. As for *A. astroticta*, Young stated that it is known in Hawaii from only a few captures, and that most were taken on the bottom in trawls, while small individuals were sometimes taken in midwater. Our samples were adults. Young commented as follows: "It is a displaced midwater faunal element, or an animal having the distinctive adaptations of a midwater animal but which seems to migrate along the bottom. The *Histioteuthis* is also a vertical migrator that stays below about 150 meters." (See Table 3). John Walters (see footnote 6) commented that the shrimp *Sergia fulgens* is an enigmatic form known only in the adult form (ours were adults) from night tows.

Morning Shoreward Movement

After nighttime feeding, spinner dolphin schools turn toward shore, ultimately congregate in certain sheltered locations where the schools subside into the rest pattern. In the case of the radiotracked animal, this movement toward shore seemed to begin at about 0300 and to consist of a gradual movement that zigzagged ever closer to shore.

The directions from which schools come into Kealakekua Bay suggest that the movement toward the coast may be a general one and not necessarily pointed precisely at a rest cove. Some entering schools first swim along the coast, round Palemano Point at the south tip of the bay, and enter the bay over the shallows near Keei and Napoopoo (Figure 1), while others enter the bay directly from the open sea, coming in at various angles to the trend of the coast. Still others enter from the north, once again after a traverse of unknown length along the shore to the north of the bay. More schools enter along the southern limb of the bay than from the north or center. The true figure for south entry may be even higher than the figures indicate (58% for south entry vs. 14.5% for

north entry; 27.5% entered in the middle sector), since some first sightings were made close to the cliffs at the back of Kealakekua Bay and, because of their location, were placed in the second sector records. It is likely that some of the schools entered from the south or north prior to the beginning of observation.

These congregation patterns suggest that the bays and coves used for rest periods may not necessarily be the direct target of daily inshore movement. The bays seem simply to collect schools that accumulate along the coast after a night's feeding. The fact that more schools arrive from the south than from the north may reflect the nearby presence of adequate resting areas over the rather extensive shallow-water areas immediately north of the bay between Keikiwaha Point and Keauhou. Waters to the south of Kealakekua Bay are deep close to shore and only very modest sized shallow coves exist at Honaunau and Hookena. Farther south, along the 20 km stretch of coast between Hookena and Milolii, no spinner dolphins were seen although both flights and ship searches were made. Nonetheless, data from marked animals show movement between the populations on each side of this gap. Unless rest areas are encountered, dolphin schools remain transient. This does not preclude the possibility that the animals may be familiar with the various rest coves or actively seek them when nearby.

Arrival times (Figure 12) concentrated between 0600 and 0950 h, though some schools arrived much later in the day. The early arrivals typically subsided into rest and spent the majority of the day in the bay. Later arrivals (those entering between 1100 and 1700 h) tended not to form resting schools and often moved out of the bay after a brief stay. The late afternoon arrivals may have completed a rest period elsewhere and then entered the bay as part of a longshore movement prior to going to the feeding grounds. Dolphins engaged in such longshore movements have been followed out to sea. In one such case a school rested, left the bay to the south, traveled slowly very close to shore until the small cove at Honaunau was encountered, and then turned out to sea as dusk approached.

Not all dolphin schools encountering Kealakekua Bay enter it. We occasionally saw schools crossing the bay mouth and swimming on in either direction. Our impression is that this occurred when other schools were deep in the bay, but unfortunately, adequate records to document

⁶Richard Young (Professor of Oceanography, University of Hawaii) examined and identified stomach samples from our Hawaiian spinner porpoise in 1973 and provided notes on the occurrence of squids in the samples, while John Walters (University of Hawaii) provided identifications of shrimps.

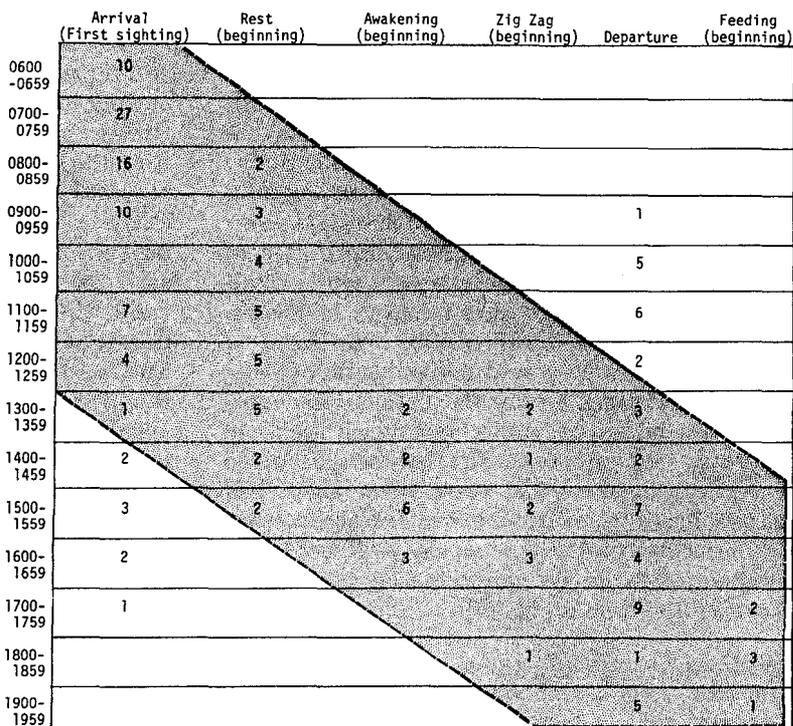


FIGURE 12—Cumulative record of time of first sighting, onset of rest, wakening, etc.

the point were not kept. Our efforts at listening to dolphins in Kealakekua Bay showed that dolphins at the mouth of the bay can easily hear those in its deepest recesses, so the effect may be one of exclusion of the passing school by occupants. The point needs further study.

Small schools often seemed to coalesce upon arrival in the bay. This first became apparent when our estimates of school size during an arrival sequence increased sharply, or even doubled, between the time the animals were at the bay entrance and when they were deeper in the bay. In other records such obvious increase in school size occurred after the animals were deep in the bay. The arrival of such supplementary schools was occasionally observed and their coalescence into a single school noted.

School structure during entry was best observed in those that entered in the central sector, without the visual interference of headlands or the swells and breakers that sometimes obscured sightings close to shore. Such schools were sometimes first seen as far as 4 km beyond the bay and could be watched during the entire entry traverse. These schools typically swam in a ragged rank composed of quite discrete groups. The dolphins were often quite active, and their passage was accompanied

by spins and other aerial behavior. Often, by the time the bay mouth was reached aerial behavior had subsided considerably, though it often persisted to some degree for as long as 2 h after initial entry. In small schools of approximately 6-15 animals, entry was often quite unobtrusive. In spite of a conscientious watch from the cliff top during early morning hours such small schools were sometimes seen first deep in the bay. Large schools typically exhibited more aerial activity than small ones, and it appeared to persist for a longer period.

Arriving dolphin schools often come to the bows of vessels where they engage in assisted locomotion or "bowriding" (Norris and Prescott 1961). Even so, if a vessel pursued such schools, repeatedly making passes through their ranks or changing speeds upon approach, the school usually edged toward deep water, and if the harassment continued, the school left the bay. Observers on shipboard usually failed to note the effect on the school as a whole, since their attention was focused on the bowriding animals. But an observer on the cliff above the bay, watching the entire school, could quickly discern this retreat. This effect nearly always occurred, even if the intruding vessel moved very carefully. Later, when the school had subsided into quiescence, it was much

more difficult to disturb the animals sufficiently to cause them to flee the bay. Even persistent attempts to enter their ranks merely caused avoidance and often a transitory flurry of aerial activity (Figure 13).

Defecation was a common feature of arriving schools, prior to subsidence into rest. From the underwater viewing vehicle the olive colored trails of semiliquid fecal material were often seen streaming from the dolphins. Three or four animals sometimes defecated simultaneously within the field of view of the vehicle. A rate for one 40-animal school was calculated at one defecation every 15 s. Presumably this rather short defecation period is related to nighttime feeding and early morning digestion. The trailing animals of a school swam through the dispersed clouds of feces with no evident reaction.

Subsidence Into Rest

Once a spinner dolphin school arrives deep in Kealakekua Bay, it normally subsides slowly into

rest, a process sometimes requiring 2 h or more. This process is so gradual and so affected by features such as school size and the time of day, that its precise onset was difficult to assign (Figure 13), and an arbitrary definition was necessary. Because rest involves the cessation of aerial behavior by all school members, we defined rest as occurring when a 10-min observation of the school revealed no aerial behavior. Occasionally, even this criterion was confounded because aerial behavior is, to some extent, "infectious," and a school subsiding into rest may sometimes exhibit 10-min periods without aerial behavior followed by periods in which some aerial activity occurs in several animals. But, generally, once a school was quiet for 10 min, little or no aerial activity occurred until arousal. Typically arriving schools were in ranked form, with group structure evident. Such schools often moved quickly (5-8 km/h) and swam resolutely, with considerable aerial behavior. Little time was spent below the surface. Dives were brief (Figure 14). Once such a school arrived at the back of the bay, under the lava cliffs,

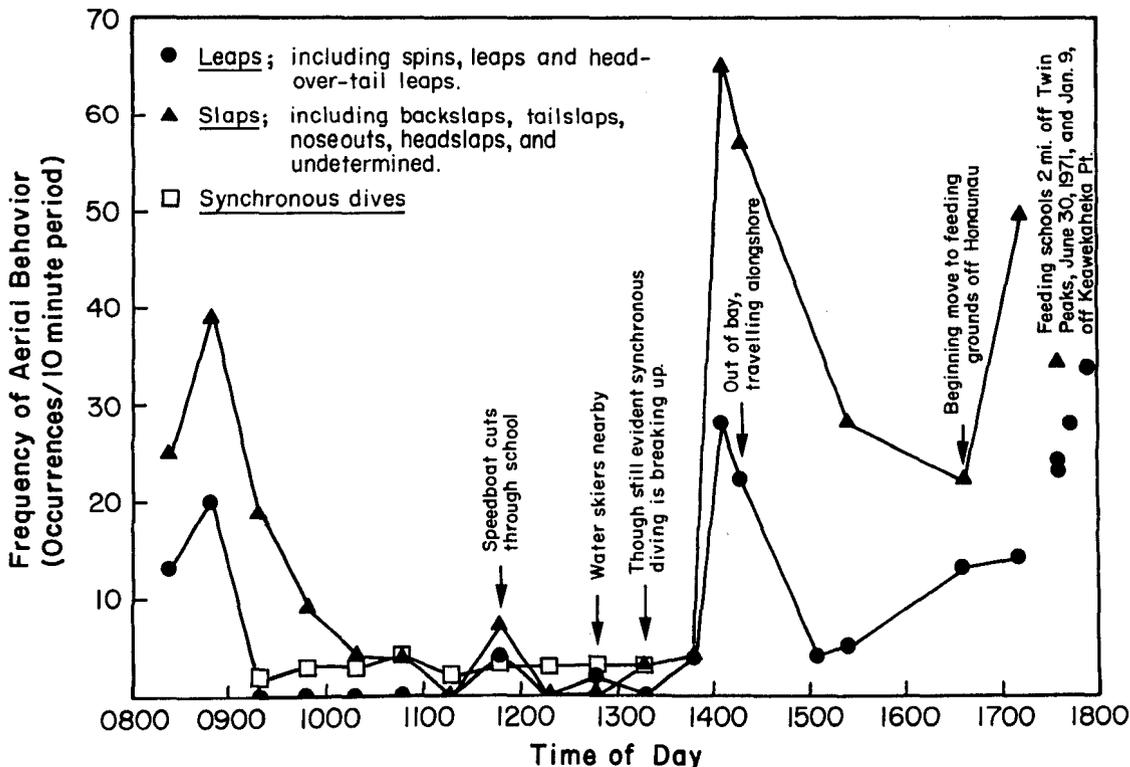


FIGURE 13.—Aerial behavior per 10-min interval for a spinner dolphin school of approximately 40 animals, 30 June 1971, Kealakekua Bay, Hawaii. Synchronous dives define the rest period, broken briefly by the speedboat. See text.

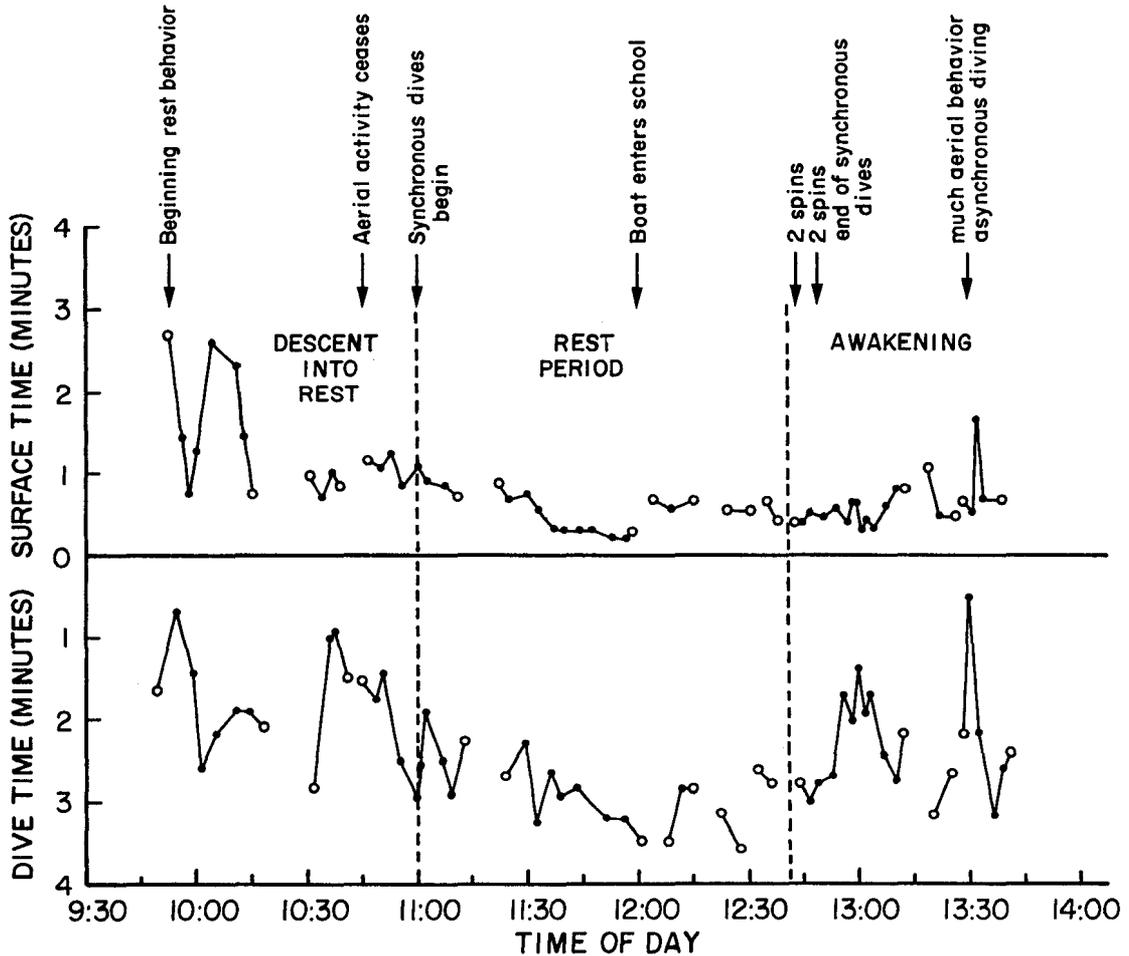


FIGURE 14.—Trends in diving and surface times in a 40 animal school of spinner dolphins, Kealakekua Bay, Hawaii, 2 May 1970. Breaks in record represent loss of the school by the observer, when a surfacing and descent was apparently missed.

it moved back and forth across the width of the bay. Its traverses sometimes took it nearly to Kaawaloa on the north and to Kees on the south (Figure 1). The various classes of aerial behavior slowly disappeared in a rough graded series: the most athletic patterns such as spins and tail-over-head leaps first, then head- and backslaps, then tailslaps, and finally all but an occasional noseout was gone.

School size and shape gradually changed at the same time. The ranked school shifted into a sub-discoidal shape and tightened markedly. For instance a school of 30 animals that once formed a spread rank over 75 m of water might become concentrated in a 20 m diameter disc. Movements became leisurely; in fact, the surface excursions of the schools became almost surreptitious as the

animals rose quietly from the depths, breathed once or twice, and descended again. It became very easy to overlook them, and two or three observers were needed to produce a complete record of their dive sequences. During rest most time was spent underwater (Figure 14).

Vocalization was at a high level in arriving schools and subsided as the rest period approached. Arriving schools made a variety of noises including click trains, burst pulse signals such as squawks or barks, and pure-tone whistles or squeals. All but clicks ceased during rest.

Rest

During rest, quiet spinner dolphin schools moved slowly back and forth, deep in the bay.

Their excursions were entirely confined to shallow water (about 3-50 m). Only when disturbed or when rest was over did the schools begin to edge into deeper water. For instance, resting schools seldom ventured into the deep channel that entered the bay at Kaawaloa, but instead moved mostly back and forth between our observation station #1 and Napoopoo (Figure 1), an area of shallow sandy bottom dotted here and there with isolated coral heads.

Resting schools often changed direction underwater, which made it difficult to predict where they would surface. Interindividual and intergroup distances gradually decreased as rest deepened, until many animals were very close to or actually touching one another, while the arriving school showed evident group structure and independence of both movement and diving time within the school; the resting school swam in much closer synchrony. Arrival of synchronous diving by an entire school provided a good, if arbitrary, indicator of the onset of rest.

On a few occasions we were able to watch synchronous dives from the MOC. The underwater vantage point allowed the observer to see subgroups of animals in the school as a whole. Tight, uniformly oriented groups dove slowly, with measured tail beats, toward the sand bottom below; leveled out a few body lengths above the bottom and moved slowly along, schooled tightly; and swam largely without individual exploratory movements. Occasionally an animal descended to the bottom and beat boils of sand up into the water with its flukes. At the end of a dive the animals rose rather steeply to the surface, not as a single tightly integrated group, but more or less seriatum, as a column of subgroups. Often after rising, the animals spread outward from this rising column a short distance before turning to define the compact confines of the surface school, like the petals of a flower opening. Once on the surface, group structure could be seen, but the animals seemed much more regularly spaced than is the case in active schools. Diving, too, was steeper and slower than in travelling groups. While individuals in resting schools seemed less alert than animals in feeding or travelling schools, the resting school itself was very wary of strange features of its environment. Any strange object placed in a rest cove, such as a buoy, boat, or line was avoided for a matter of days before a school seemed to habituate to its presence. It was striking that they reacted to foreign objects in

much the same way as we have come to expect from fish schools, and not with typical dolphin individuality. For instance, when a resting school cruised inshore of us near the cliffs, we waited in a quietly rocking skiff some 75 m offshore, and the school approached slowly as a discoidal group, thinned as it reached a point directly inshore of us, streamed between the skiff and the cliff as a long line of quietly moving animals, and reformed its discoidal group once past us. We found that our skiff or our anchored workboat could deform such discoidal groups from some distance, causing the side nearest the skiff to become dented or malformed as the entire school reacted to our presence. When a four-hydrophone array capable of sound triangulation was placed near the path of such resting schools, it was assiduously avoided and no animals were known to pass through it for 6 days after its placement (Watkins and Schevill 1974). A line stretched across the surface of the water was capable of deflecting such schools. In such cases, even though the animals moved slowly and other evidence of alertness, such as complex phonation or aerial behavior, was nearly absent, the school as a whole remained alert. We suppose this is due to sensory integration by the closely packed school, that is, by the reception of environmental information by some members of a school and transmission of its occurrence to all or most of them. It was usually possible to cruise among alert schools, and many individuals might station at the bow within a few feet of an observer, but resting animals very seldom came to a vessel.

A graphic demonstration of spinner dolphin's fear of strange objects was given by our attempts to encircle quiescent spinner dolphin schools with a modified Hawaiian "hukilau".

Our hope was that this fear might be utilized to assist in their release from tuna seines, since at the time large numbers were being killed per year in the yellowfin tuna fishery. We conceived that light weight gear of this sort could be deployed in a tuna net to crowd the captive animals, and thus assist in their release. Our tests, run in August 1973 in Kealakekua Bay, used a hukilau composed of 450 m polypropylene cork line ($\frac{1}{2}$ in; 1.27 cm) from which were hung every 2 m, thin poly-

⁷A hukilau is a Hawaiian "net" made of a cork line with palm fronds woven through it at intervals, which is towed across coral areas, chasing fish in front of it. Because a mesh net is not involved, it does not entangle on the rough bottom but still serves to concentrate the fish, which are then netted from inside the hukilau over sandy bottom.

prophylene lines ($\frac{1}{4}$ in; 0.6 cm) 18 m long (Figure 15). With this insubstantial barrier we were able to encircle whole schools of spinner dolphins in 20-40 m of water and to crowd them severely. In one case when the hukilau was reduced to a surface area of 6×10 m, a school of 40-60 animals refused to leave through the wide openings but continued to mill inside (Figure 15). Even when two of the thin vertical lines were removed, leaving a "door" 6 m wide, the school continued to circle, "eyeing" the opening but not passing through it. Only when the area was further reduced did the majority of the animals pass through the wide opening. They had been held captive for 3 h 50 min in this fashion.

Although large and small schools may become quiescent, sporadic low intensity aerial behavior may continue. The impression given is that very small schools (ca. 6-12 animals) maintain a degree of individual wariness, perhaps related to the uncertain protective effectiveness of their few members, while very large schools may always contain some alert animals. For instance, based on a small number of observations in the large (100-150 animals) schools seen at Keahole Point, we have never noted deep quiescence. It is as if the members of the small school were afraid, and that some activity always occurred somewhere in the larger schools. Only schools of about 20-40 animals seem to achieve the most complete quiescence.

Even though aspects of diurnal behavior sequences were recorded on 83 days, complete sequences were recorded on only 13 days. Based on these observations, rest periods ranged from 41 min to 6 h (mean = 3.62 h).

Once quiescent, resting schools are rather difficult to disrupt. Several times cruise boats or water skiers went through resting schools during our observations. The usual result was a brief flurry of low-level aerial behavior, for example, a desultory headslap, an imperfect spin, and then the school would subside into complete quiescence again (Figure 13).

Arousal

Arousal, unlike descent into rest, is abrupt, both in terms of school dispersion and aerial activity. In a completely quiescent spinner dolphin school, arousal was marked by sudden active aerial behavior—a complete spin or headslap, for instance. Within 10 min of such initial aerial activity the school was often fully alert, with aerial

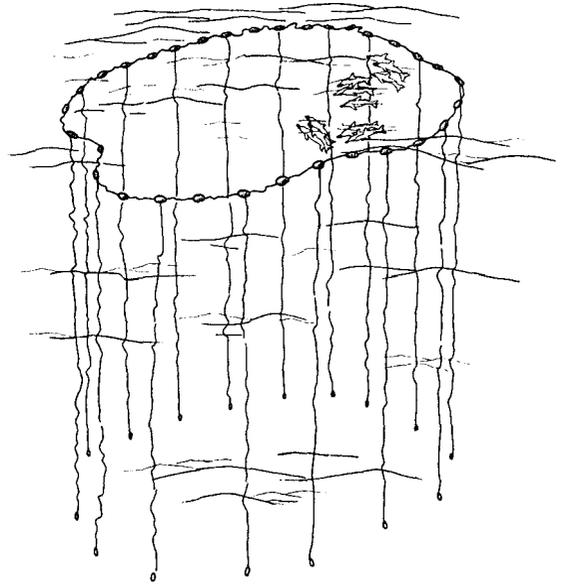


FIGURE 15.—An Hawaiian "hukilau" composed of a cork line and hanging vertical weighted lines, showing a school of spinner dolphins held inside. Vertical lines are 3 m apart and 20 m long. See text.

activity high throughout the school. In fact, the highest levels of aerial activity recorded occurred at arousal, and later, during feeding (Figure 13).

Zigzag Swimming

At arousal the pace of the spinner school quickens. Group structure suddenly becomes obvious again. At arousal the school moved back and forth across the bay, or sometimes in and out from the bay center to the cliff base. In either case the school often began to traverse deep water. Typically, it swam toward the bay mouth beginning with a flurry of activity and speed, often with animals rushing through the water, creating spray and small bow waves as they raced along. As the bay mouth was approached, usually the school gradually slowed and finally began to mill then turned back into the bay. Sometimes the school then subsided into further rest, or accelerated again, often toward the opposite side of the bay. This entire pattern is what we have termed "zigzag" swimming. These patterns, we suspect, are, to some extent, influenced by the topography of Kealakekua Bay, and may take somewhat different expressions elsewhere.

Spinner dolphins were observed moving in zigzag fashion at Kealakekua Bay, in and out and from headland to headland. The longest bout of

this behavior took 2.75 h. Typically zigzag swimming ended with fast swimming that took the school beyond the confines of the bay altogether. It was as if one had been rocking a blob of mercury in a bowl, and a final strong motion sent the blob flying, completely free of the bowl.

If the animals left the bay early in the day, the school usually traveled close to the shoreline, either to the north or south, and later in the day, turned toward deep water offshore. When a school left the bay near dusk, it usually headed directly out to sea.

As exodus from the rest location began, schools traveled either as ranked schools (wider than long) or in straggling lines arranged in more or less linear fashion. As the school moved offshore, it spread. It sometimes coalesced with other schools moving in the same general direction. By the time feeding grounds were reached, usually near dusk, a school that, during rest, had formed a 25 m diameter disc might have expanded until its groups were scattered over a kilometer or more of sea. As noted earlier, we have estimated some feeding schools as 3 km in breadth.

Social behavior, including mating, aerial behavior, sexual play, and aggressive chases, becomes especially evident in spinner dolphin schools moving toward the feeding grounds. Once there subsynchronous feeding dives begin.

Dive Patterns

An example of the daily cycle of dive patterns is shown in Figure 14. As animals entered the rest area, the pattern was one of short dives, with most time spent on the surface. Then this pattern gradually shifted as dives became longer and surface times shorter. When the school was near or over the shallow area where rest occurs, dives become synchronous, or nearly so. During arrival the groups of a school, especially if it was a large one, often dive out of synchrony with one another. During rest, as shown in Figure 14, the duration of dives continued to increase until the longest dives were approximately 3.5 min duration; surfacings at that time were brief, between 10 and 30 s duration. Throughout the rest period, the school, if it is small or moderate in size, dives in synchrony. During the arousal period, surface times gradually increase while dives tend to become much more variable in length than during rest. Finally, as the school travels out to sea, individualism reaches its peak, with animals scattered in pairs or small

subgroups, or even alone, within the envelope of the school as a whole. Synchronous diving is lost as movement is at or close to the surface and directed into horizontal travel. Then, on the feeding grounds, when the school is at its most dispersed, the scattered school slows and begins synchronized diving again, presumably to feed. Internal factors, such as the return to equilibrium after a dive might play an important role in determining diving patterns. As for mediating signals, the cessation of aerial behavior in an area of the school that has dived could signal adjacent school segments that diving is occurring; or, vocal signals could mediate it, and thus a wave of information about a dive in progress could travel across the school. The high incidence of aerial behavior in feeding schools and the lack of precise synchrony in feeding dives support such a speculation.

Social Behavior

Social behavior in wild spinner dolphin schools has thus far proved all but impossible to observe in an orderly fashion. Glimpses of individual animals or subgroups are fleeting, and the opportunity to identify individuals or their sex is sporadic. Hence, the observations that follow are highly fragmentary.

Mother-Young Behavior

Very small calves are always seen in the company of adults. However, young spinner dolphins of quite small size (about 1.2-1.7 m TL) may form groups within a school with no evident adults in close attendance. Newborn calves with adults have been seen at all seasons of the year (Figure 16), as have groups of unattended larger calves.

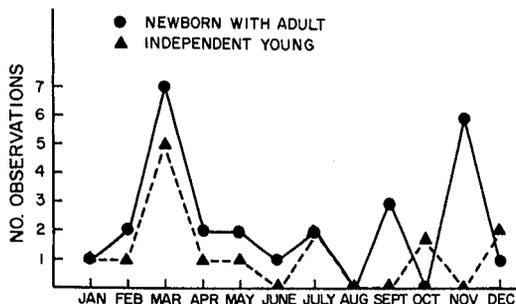


FIGURE 16.—Annual occurrence of newborn in spinner dolphin schools off Hawaii (1968-72). Only sightings of newborn with evident fetal folds are included.

Nursing has seldom been seen in nature. In one cliff-top observation, a 60-animal school swam below, containing a group of adult-calf pairs. One of these pairs engaged in nursing. The adult turned slightly on her side as the young dolphin positioned itself obliquely alongside with its beak pressing against her at the mammary slits. The behavior persisted for a few seconds before the animals dove. The posture was like that reported in captive dolphins (Dohl et al. 1974).

For 33 days in February-March 1970, a female pair was seen in Kealahou Bay and nearby Keauhou. Unlike most such pairs, the two often swam near our observation vehicle. The calf had the distal 5-6 cm of its rostrum broken through and bent to the side with some ragged flesh exposed. In spite of this apparently grievous wound the calf appeared active and well nourished. Contact was very frequent between mother and calf. Both the adult and calf used their flukes, flippers, and dorsal fin to achieve this contact. On two occasions the young animal touched its dorsal fin to the adult's flank, laid its flukes up under and touching hers, and held this position as their combined tail beat propelled them both along. The young animal rode both above and below the adult, sometimes directly beneath her midbelly, occasionally sliding backward until the moving flukes of the adult tapped against its dorsal fin. In our observations we never noted true assisted locomotion as described by Norris and Prescott (1961), though

swimming speed was generally so slow that it might not be expected.

A common posture was for the baby to swim below and a little to the side of the big female, at which time she placed her flipper against the young animal's back, just anterior to its dorsal fin. Much of the time the pair in this position swam in synchrony, turning and diving together.

On occasion the young animal swung away from the adult for a few meters but soon turned, increased speed, and rushed back to her. Once, during a particularly long sortie, the adult pursued the calf, slapped its back with her flukes, and then the pair dove together.

Sexual Associations

At times, both on a given day and over several days time, specific subgroups of 2-6 spinner dolphins whose members could be individually recognized, were seen together from the viewing capsule. It was possible to determine the sex of some of the animals. Sexually related behavior was exhibited between male and male and male and female pairs. It takes several forms. What Bateson (see footnote 5) called "beak propulsion" was noted (Figure 17). In it one animal swam up from below another and inserted the tip of its rostrum into the genital slit of the upper animal, apparently pushing the passive animal along. Both the dorsal fin and the flippers are commonly used to stroke or

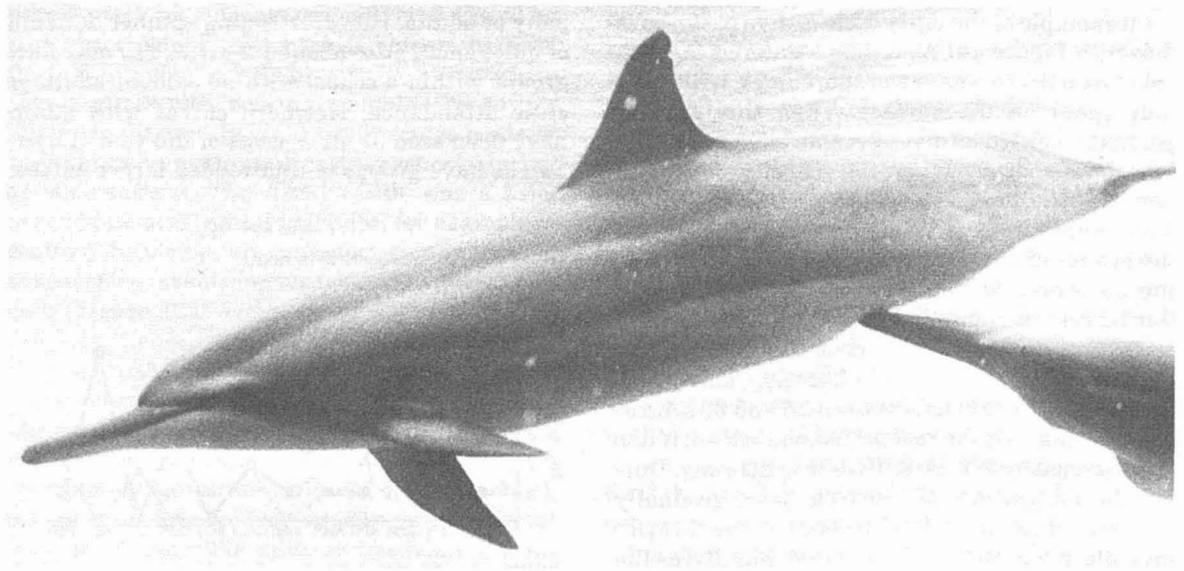


FIGURE 17.—Beak propulsion by a captive pair of spinner dolphins at Sea Life Park, Hawaii. An adult female is pushing an adult male.

probe the genital area of another animal, and the upper animal sometimes rode along with the dorsal fin of the lower animal pressed into its genital area. Mating postures were commonly seen, most often in alert schools early in the morning or near dusk. On one occasion (in captivity) we were able to determine that both partners in such a pair were males, even though females were present in the tank. We were able to confirm heterosexual contact in some pairs in nature. Typically, one animal swam in the normal upright orientation while another swam upside down, with the genital areas of the two pressed together. Either sex could be above or below. Intromission was usually difficult to see, but was noted on occasion. Contact was sometimes maintained for several seconds. In some observations the upper partner was relatively quiescent and propelled itself with fluke strokes of much reduced amplitude compared with those of normal swimming. One mating chase was noted as a school moved onto the feeding grounds off Keauhou, the pair raced by the bow of our vessel as we travelled at an estimated 4 kn. They dove and spiralled swiftly together. The coupling and synchrony of movement of the pair was so perfect that the two animals were not evident until the pair turned on its side. Together they veered away from the bow, diving about 20 m down and remaining in the coupled position for several seconds. We heard whistling with the unaided ear when such coupled animals were near the ship.

A particularly complete observation of mating was made from the MOC on 26 July 1970, at Kealakekua Bay. A male-female pair swam directly in front of the viewing capsule, and the female swam under the male until their ventral surfaces were in contact. The penis of the male was seen to enter the female, though no thrusts were noted as the position was held for 3-5 s, while the animals glided without fluke strokes, and then the animals parted. Shortly, the female again moved under the male, but no further intromission appeared to take place. Instead, the male accelerated with a few fluke strokes, and the pair cruised off, side by side.

Competition for partners was occasionally observed. On 29 March 1970 at Kealakekua Bay, the MOC entered a school of 12-13 animals, and 2 were noted swimming upside down. Both pursued and came up under a single adult above them. Later, three inverted animals pursued two in the normal swimming posture. At that moment another large

adult swam rapidly to the moving group and forcefully inserted itself between one inverted animal and the one above it. The upper animal then dove away from the group, with the intruder following. The two inverted animals moved quietly, maintaining their upside-down orientation, toward another nearby animal swimming in normal orientation.

Observations of captive spinner dolphins show that much social interaction is sexually related and that it may occur between animals of all age classes and combinations of both sexes. As has been found in the Atlantic bottlenose dolphin, *Tursiops truncatus*, sexual behavior and social communication are interwoven to such an extent that it is often impossible to separate true courtship and mating behavior from communicative behavior of other sorts. For example, Caldwell and Caldwell (1967) reported a 2-day-old male Atlantic bottlenose dolphin having an erection when brushed by its mother. Sexual maturity is not reached in the spinner dolphin until a minimum of 3.7 yr (Perrin et al.⁸) and even later in the bottlenose dolphin, and thus one must view this precocious use of sexual patterns as part of the development of communication concerning relationship. Such communicative use of sexual patterns has been reported for mixed schools of captive spinner and spotted dolphins (Bateson see footnote 5).

Other Social Patterns

Contact, not necessarily sexual in context, is common between members of dolphin schools. When groups of animals swam near the viewing capsule, one could often see animals touching one another with the tips of pectoral fins, the dorsal fins, or fluke tips. Jostling or pushing of animals near the capsule often occurred and was accompanied by sound emissions. Such jostling can be seen commonly in other bowriding groups. Because a few animals from a given school seem to do most of the riding and some seem to occupy specific places at the bow, one gains the impression that hierarchical relations in the school are involved.

The release of air may correlate with social signals in spinner schools. Commonly, long streams

⁸Perrin, W. F., D. B. Holts, and R. B. Miller. 1976. Growth and reproduction of the eastern spinner dolphin. A geographical form of *Stenella longirostris* in the eastern tropical Pacific. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Admin. Rep. LJ-76-13, 84 p.

of air were noted issuing from the blowhole corners in spinners near the capsule. Whistles and chirps could often be heard concurrently. Sometimes, during active chases one or more animals would release a large bubble of air underwater, which boiled upward to the surface. Pryor (1973) has correlated such behavior in captive animals with frustration.

Spinner dolphins change school swimming patterns in relation to weather. In rough seas, groups of dolphins appear to ride the swells and breaking waves that sweep toward the Kona coast. On one such occasion, while we "hove to" in a rough sea, perhaps 100 spinners passed us. They were divided into small groups of less than a dozen animals. These groups swam tightly together and often could be seen racing down the foreslope of the waves, sometimes breaking the water together and sometimes staying wholly within the wave. Such behavior is commonly seen in other cetacean species (Norris and Dohl in press).

Sound Emmissions

A detailed study of spinner dolphin sound emissions will be presented in a future paper. A few observations are appropriate here.

There is a marked diurnal fluctuation in the kind and amount of spinner dolphin vocalization (Powell 1967). Alert schools produce an array of sound types such as clicks, pure-tone whistles or "squeals," and a variety of burst pulse signals that can be described by such terms as barks, moos, chirps, etc. The clicks are of considerably lower intensity than either the whistles or the burst signals (Watkins and Schevill 1974), and the clicks may be more tightly focused.

Resting schools are nearly silent, emitting almost entirely clicks and even these are sporadic. Simultaneous with arousal, vocalizations rise in variety and abundance. Whistles and burst pulse signals can be heard quite long distances underwater. With Watkins and Schevill, we were able to station ourselves outside Kealakekua Bay and hear whistles and various burst pulse signals from a group of spinners swimming close to the cliff, approximately 2 km distant. Thus, a school of dolphins swimming outside Kealakekua Bay during longshore movement would be able to detect animals deep in the bay without entering it. It is possible that the schools we have seen passing the bay when others occupied it may have been excluded by acoustic signals.

No context-specific sound signals have been identified by us, except that it seemed clear that clicks were emitted concurrent with the inspection of the environment. The likelihood of context-specific acoustic signaling in the daily events in the school, however, seemed high. For example, synchronous diving in very widely dispersed schools, or simultaneous turning of an entire school at dusk, are unlikely to be visually cued (though it is not impossible). The sounds produced by aerial behavior have, in a few instances, been picked up by our listening gear. Tailslaps are especially loud, while spins (which we have recorded in captive situations) produced a lower intensity signal quite different in character.

Predators

Hawaiian spinner dolphins seem to be attacked with some frequency by sharks. Several of the scarred animals we cataloged had obviously been wounded by large sharks. Lunate rows of tooth marks, especially on the tail region, some apparently from sharks with a 12-15 in (31-38 cm) gape were noted. In one case it seemed that the entire tailstock had once been in a shark's mouth. Nicked or tattered dorsal fins may also have been produced by shark bite.

Subcircular scars somewhat larger than a silver dollar commonly seen on tropical and subtropical cetaceans are common on spinner dolphins. Jones (1971) suggested that these scars are produced by the small squaloid shark *Isistius brasiliensis*. This small shark occurs with scattering layer organisms, is bioluminescent over its entire body, and is thought to be a squid mimic. Feeding dolphins may be attracted to it, and when close, the shark may swim to the dolphin, attach itself, and then scoop out a disc of blubber and flesh with its peculiar dental and branchiostegal apparatus. The shark has erect cutting teeth only in the lower jaw and a jaw apparatus that allows it to attach and push the teeth through the flesh of its prey like a cookie cutter. The shark may bite while facing the tail of the porpoise and be swung around in the current, cutting as it goes. Discs of dolphin blubber have been found in the stomachs of this shark (Jones 1971). We have seen fresh wounds of this shape and size several times, including some completely through the blubber to the flesh beneath. Nearly every adult dolphin bears some scars of this sort, on some part of its body. We have never seen such scars on the appendages or head, though

they are common on the throat, flanks, and especially on the belly and the region between the flippers.

DISCUSSION

Instead of finding tightly knit schools of constant size that habitually occupied a given cove, as we had expected we found coves occupied by schools of highly variable numbers and composition. These variable schools often merged with other schools to form large feeding groups offshore, and school members moved back and forth between resting areas many kilometers apart in what seemed a completely free fashion. Rather than finding dolphins occupying a "home cove" the tendency to gather in shallow waters near shore seems to be related to a combination of topographic factors including the presence of adequate areas of shallow water and the proximity to nearby deepwater feeding grounds. Further, the population occupying such a cove during the daily rest period seems limited in some fashion by this same topography. Kealakekua Bay seems able to hold only about 60-70 animals, and even this number seems so large that rest may be inhibited. Deep rest, without aerial behavior, seems only to occur when relatively few animals, about 30-40 or less, are in the cove. In contrast, Keahole Point regularly holds >100 animals during daily rest.

Instead of finding schools headed directly for rest areas in the morning, we found schools moving toward the coast in the morning in a much more general fashion, encountering the coast, swimming alongshore, entering coves, sometimes coalescing with schools already in occupancy, or apparently sometimes passing by a cove filled with animals, to move on toward other less occupied rest areas. The entry and exit patterns of schools relative to coves also suggests such opportunistic use. At Kealakekua Bay, schools entered primarily from the south perhaps because rest areas south of this bay are very restricted while much more extensive areas exist to the north and in effect this inhospitable shore "collects" but does not hold incoming schools. Exit, on the other hand, is primarily to the north, as if schools came into the cove rested for a time, and continued on their way toward offshore feeding grounds. The primary feeding grounds seem to be to the north and west of Kealakekua Bay, off the shallows of the island, though our observations are sparse. To the north of Kealakekua Bay are other rest areas, while to

the south deep water adjoins the shore. Thus occupancy or lack of same of a given rest cove and arrival direction to it may be related to nighttime feeding movements which leave animals offshore at various locations after the scattering layer descends with dawn. None of this, of course, indicates that dolphins do not know where available rest areas are, or know the features of them.

What, then, is the true dolphin school? Are the large offshore aggregations, formed of a coalescence of smaller resting groups, such a cohesive unit? Or, should we focus our attention on school subgroups of a few animals, which may habitually swim together (though our evidence is inconclusive in this respect), in the search for structure, regarding the large groups as opportunistic assemblages? Or, can both be properly considered as schools?

The large offshore feeding assemblages have clear structure in some respects. Such schools often dive and surface more or less together, and much social behavior is evident at times in them. These schools swim in a common direction and sometimes change course in a coordinated fashion. We often noted age-related subgroups within them; mothers and calves, or juveniles swimming together. But, if such schools are followed, they will sometimes split into parts that move in different directions, and clearly, they fragment during the day when smaller schools enter coves or shallows to rest.

Smaller schools exhibit most of the same behavior, though many times not all age classes will be represented in them. Schools of less than about 30 animals are seldom split for long by a vessel. These groupings we call schools, preferring to recognize that such schools change in size from time to time.

Clearly, from our marked animal information, individuals utilize a rather extensive area of coast for feeding, moving from group to group, and thus, in aggregate the population of a given portion of coast is a functional unit, in relation to its trophic relations with the immediate environment. The degree of discreteness of such populations from those adjacent remains wholly unknown, as does any possible intermixing between islands.

Considering this high degree of fluidity, how is directed movement of a school achieved and how does the structure of schools come about? No leader seems to exist in the standard sense of an animal determining direction of movement by

swimming at the head of a group. Yet directed movement does occur in cetacean schools. Killer whales arrive off sea lion and sea elephant rookeries at the proper time to catch pups (Norris and Prescott 1961), and pilot whales arrive at specific feeding grounds when squid come to spawn or when capelin arrive in large schools (Sergeant and Fisher 1957). Such patterns presumably have a learned component, and similar patterns of dolphins opportunistically using human activities to locate and capture food must be largely or wholly learned. For instance, bottlenose dolphins follow trawlers in the Gulf of Mexico (Leatherwood 1975) and in the Gulf of California (Norris and Prescott 1961) and obtain fish and other food items stirred up by the trawl or cast over the side during sorting of the catch.

Tavolga and Essapian (1957) described adult male bottlenose dolphins harassing newborn calves and their mothers, and dominance by adult females is also discussed. We have noted strong aggressive behavior in captive male spinner dolphins at Sea Life Park oceanarium in Hawaii. In the wild dolphin school, similar actions probably serve to order the structure of the school. Females and newborn young may be herded to their normal position in the interior of the school. We expect that such aggression combined with experience may serve to regulate the direction of school movement from various locations in a school. For instance, adult male killer whales usually occupy a position in travelling schools far out on the wings of the moving group, and from this position directional signals may be communicated to the school as a whole (Norris and Dohl in press).

The tendency of spinner dolphins to rest over shallow sandy areas is most probably a protective adaption allowing the quiescent school to place a protective bottom close beneath it and a shore nearby on one flank. The chances of attack from those directions by large deepwater sharks are correspondingly reduced. With much individual behavioral flexibility suppressed in resting schools, collective wariness rises, we presume through sensory integration by the school. Thus, the use by spinner dolphins of alert daytime-feeding spotted dolphin schools in the open eastern tropical Pacific Ocean, we feel, may account for the otherwise unusual daytime association between these two species.

We regard this study as preliminary, allowing glimpses into the life of one wild dolphin species and focusing our attention on important problem

areas such as acoustic signalling, school structure, energetics, and social relationships.

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